

Proc. Roy. Hort. Soc. London 3: 200. 1863 = *Phryganocydia coito* var. *platypoda* (DC.) Bureau, 1893 [Vol. 55]: 111. 1894.

TYPE: Brazil. Bahia, 1834, *J.S. Blanchet 1511* (holotype: G-DC [G00133644] image!; isotype: P [P03577088] image!)

Macfadyena riparia S. Moore, Trans. Linn. Soc. London, Bot. 4: 417. 1895.

TYPE: Paraguay. Between Santa Cruz and Villa Maria, December 1891, *S.L.M. Moore 837* (holotype: BM [BM000992372] image!)

Macfadyena bangii Rusby, Bull. Torrey Bot. Club 27: 71. 1900.

TYPE: Bolivia. Junction of Rivers Beni and Madre de Dios, August 1886, *H.H. Rusby 1139* (holotype: NY [NY00278054]!, NY as K-Neg 3382; isotypes: MICH [1210238] image!, PH-1073254 image!, US-1322457 image!)

Description: Lianas. **Stems** solid, cylindrical (sub-tetragonal), not winged, with lenticels (without lenticels), without interpetiolar gland fields, without interpetiolar ridge (with interpetiolar ridges), without simple trichomes, moderately to densely lepidote; prophylls caducous, foliaceous, elliptic, spreading or reflexed, stipitate, slightly asymmetrical, 3.4 – 18.9 mm × 2.2 – 12.9 mm, without simple trichomes, densely lepidote, with few to many glands on adaxial surface; bromeliad-like prophylls absent. **Leaves** (1–) 2-foliolate; petiole semi-cylindrical (cylindrical), 5.3 – 37.7 (– 59.0) mm, without simple trichomes (glabrescent), densely lepidote (moderately lepidote); petiolules caniculate, 7.0 – 24.5 mm, without simple trichomes, densely lepidote (moderately lepidote); blades concolor to slightly discolor, chartaceous to coriaceous, matte (laevigate), symmetrical (slightly asymmetrical), ovate (elliptic or oblong), acute to acuminate (rounded, obtuse or long acuminate) apically, rounded (cuneate, truncate or sub-cordate) basely, 8.3 – 22.7 × 2.8 – 11.8 cm, adaxial surface without simple trichomes (minutely pubescent along midvein), moderately lepidote (sparsely lepidote), with few to many glands clustered at base and apex, abaxial surface without simple trichomes, moderately lepidote (sparsely lepidote), with few or no glands clustered at base or scattered, without domatia; venation pinnate, tertiary venations alternate percurrent; tendrils rarely present, simple, without simple trichomes, sparsely to moderately lepidote, with glandular apex. **Inflorescences** compound dichasia or umbels of compound dichasia (thyrsi,

with lateral dichasia compound and pedunculate), multiflorae, corymbiform, terminal or axillary, without simple trichomes (glabrescent), moderately to densely lepidote, primary axis (when present) 132.0 – 260.0 mm long; bracts caducous, linear or triangular, $1.9 - 4.7 \times 0.5 - 0.6$ mm, densely lepidote, without glands; pedicels 0 – 7.4 mm, without simple trichomes, densely lepidote. **Flowers** with calyx spathaceous, 1-apiculate, plane, smooth, membranous, $18.2 - 38.4 \times 6.1 - 12.0$ mm wide at medium height, without simple trichomes, moderately lepidote and densely at apicule, with none to many glands at apicule, apicules 1.9 – 7.7 mm; corolla purple (white) outside, purple or white inside, infundibuliform, dorso-ventrally flattened, membranous, (39.7 –) 47.9 – 104.7 mm, externally without simple trichomes or pubescent at upper tube region, sparsely lepidote (moderately lepidote), without glands, internally without simple trichomes (pubescent at lobes and upper tube region), not lepidote (sparsely lepidote), with shortly stipitate glandular trichomes at base, tube (25.6 –) 34.8 – 75.6 $\times 2.5 - 3.9$ mm wide at base and (7.1 –) 10.3 – 22.1 mm wide at apex, lobes sub-circular (rounded), $9.7 - 30.2 \times 10.6 - 36.2$ mm; androecium didynamous, with stamens included, the largest 13.2 – 20.5 mm, the shortest 6.6 – 15.9 mm, without simple trichomes, not lepidote, with stipitate glandular trichomes at base, thecae 3.2 – 4.8 mm, staminode 2.8 – 6.1 mm; gynoecium 26.6 – 55.0 mm, ovary cylindrical, smooth, without simple trichomes, densely lepidote, ovules in 2 series per locule, style lepidote at base; nectariferous disk reduced. **Fruits** flattened, linear, $16.8 - 47.8 \times 1.4 - 2.3$ wide $\times 0.2 - 0.5$ cm thick, valves woody, without ridges, smooth, without simple trichomes, densely lepidote, without glands (with few scattered glands). **Seeds** beige or brown, slim, narrowly transversally oblong (transversally oblong), symmetrical, $12.6 - 20.5 \times 38.8 - 74.9$ mm, seed body central, flattened, 0.9 – 1.8 mm thick, wings 2, opaque.

Distribution: This species can be found in wet and dry forest in **Bolivia** (Beni, La Paz, Pando, Santa Cruz), **Brazil** (Acre, Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Rio de Janeiro, Rondônia), **Colombia** (Antioquia, Atlántico, Bolívar, Boyaca, Caldas, Caquetá, Cesar, Chocó, Córdoba, Guajira, La Guajira, Magdalena, Meta, Nariño, Norte De Santander, Santander, Sucre, Vaupes, Vichada), **Costa Rica** (Puntarenas), **Ecuador** (Napó), **French Guiana**, **Guyana** (Rupununi), **Lesser Antilles** (Trinidad, Virgin Islands, Windward Islands), **Panama** (Canal Area,

Chiriquí, Colon, Darién, Panamá, San Blas), **Peru** (Loreto) and **Venezuela** (Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Delta Amacuro, Distrito Federal, Falcon, Guárico, Lara, Miranda, Monagas, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia) from sea level to 1700 m (Fig. 20).

Phenology: Flowers abundantly throughout the year. Fruiting are more commonly collected from January to May, but are documented during the whole year.

Discussion: *Bignonia corymbosa* is characterized by densely lepidote indument that covers all organs, spathaceous calyx, chartaceous to coriaceous leaflets and multiflorae inflorescences. The spathaceous calyx is shared with *B. neouliginosa* and *B. phellosperma*, but these species differ by the pauciflorae inflorescences. The fruit is also distinct among these species: they are circular to cordate in *B. phellosperma*, linear and short (< 13 cm) in *B. neouliginosa*, and linear and long (> 16 cm).

Bignonia corymbosa is highly morphologically variable, specially regarding leaflets shape and size, inflorescence structure and corolla size. It occurs from Costa Rica to Brazil, in three main ranges: (1) Panamá to Venezuela, (2) Eastern Amazonia to Bolivia and (3) Coastal Brazil. Some characters could be used to segregate these populations, e.g., bigger inflorescences, with longer axes and calyces, and more densely flowered (pop. 1), elliptic to oblong leaflets with rounded apex and shorter fruits (pop. 2) and sessile flowers and almost winged inflorescences axes (pop. 3). However, these characters are more predominant in one of these populations, but, although rarely, are always found in the others, creating a morphological continuity among them.

Bignonia coito was described by Vellozo (1825), with a brief description and cited the plate 19. in volume 6 of Fl. Flumin. Icon. Since no original material of Vellozo is available (Stafleu & Cowan, 1986), the referred plate is designated here as lectotype.

Selected specimens: BOLIVIA. **Beni:** Hamburg, Heavily disturbed flood plain forest along road to Hamburgo, Km 1 and 2 at SW edge of Riberalta, -11.033333, -66.1, 220 m, 24 May 1982, *Solomon 7762* (MO, NY). Riberlata, Ca. 3 km SW of Riberalta on road to Hamburgo (crossing of Río Beni). Várzea forest, heavily disturbed, -11.033333, -66.1, 230 m, 20 Sep 1981, *Solomon 6336* (MO, NY). **La Paz:** Iturrealde,



Figure 21. Morphology of *B. corymbosa* (Vent.) L.G. Lohmann and *B. neouliginosa* L.G. Lohmann. **A–D** *B. neouliginosa*: **A** Habit **B** Calyx apex with clustered glands **C** Fruit **D** Seed **E–H** *B. corymbosa*: **E** Habit **F** Node with prophylls and accessory buds **G** Glands cluster at base on adaxial leaflet surface **H** Fruit. Illustrated from *Gentry 15364* (MO) [**A–D**], *Gentry 10323* (MO) [**E–H**] and *Alvarenga 527* (MO) [**F**].

Iturralde, Luisita, W of Río Beni, -13.083333, -67.25, 180 m, 29 Feb 1984, *Beck 10128* (MO, NY). **Pando**: Manuripi, Manuripi, A lo largo del arroyo Bay. Entre el campamento Bay y la Poza, -12.066667, -68.05, 17 Oct 1989, *Beck 19428* (LPB, MO). **Santa Cruz**: El Refugio, Reserva Ecológica El Refugio, a 4 hrs. de la bahía

Toledo hacia el campamento Refugio. Bosque pionero dominado por *Diospyrus* sp, -14.737222, -61.0775, 160 m, 22 Apr 1995, *Guillén 3257* (MO, NY, USZ). BRAZIL. **Acre:** Rio Branco/Porto Velho, Rodovia Rio Branco-Porto Velho, km 120-190, -9.966, -67.8, 24 Feb 1978, *Santos 168* (MG, MO, NY). **Alagoas:** Piaçabuçu, Soares. APA de Marituba do Peixe, -10.29486111, -36.40944444, 3 Feb 1988, *Moreira 80* (NY). **Amazonas:** Nhamundá- perto da cidade (na ilha), 22 Nov 1984, *KNOB 579* (MO). **Bahia:** Nova Viçosa, Dois Irmaos, Mpio. Nova Vicoso, -20.716667, -40.75, 9 Apr 1984, *Hatschbach 47750* (F, MBM, MO). **Ceará:** Crato, Floresta Nacional do Araripe, Carrasco, -7.2344, -39.4092, 6 May 1991, *Barros 76* (NY). **Distrito Federal:** Brasília, Bacia do Rio S. Bartolomeu, -15.834492, -47.708613, 29 Apr 1980, *Heringer 4545* (MO). **Espirito Santo:** Linhares, Linhares. Rancho Alto, -19.366, -40.066, 7 Dec 1984, *Hatschbach 48686* (MBM, MO). **Goiás:** Reserva Ecologica do IBGE, Reserva Ecológica do IBGE, -15.666, -47.983, 1100 m, 8 May 1989, *Alvarenga 233* (MO). **Mato Grosso:** Poconé, Mpio. Pocone. Pantanal. 50 km S of Pocone on Transpantaneira (MT060) to Porto Jofre, -17.25, -56.916, 27 Oct 1985, *Thomas 4634* (MO, NY). **Mato Grosso do Sul:** Corumbá, Baía do Castelo, 140 km de Corumba, -19, -57.64, 10 Nov 1982, *Paula 1673* (MO). **Minas Gerais:** Coronel Eneas, Fazenda Bom Sucesso (Mpio. Cel. Eneas), 17 Feb 1991, *Hatschbach 55217* (MBM, MO). **Pará:** Paraupabas, paraupabas, Reserva Biologica da Serra dos Carajas. Companhia Vale do Río Doce. Area da planta piloto, mina de exploracao de ferro-N4, -7.75, -51.5, 500 m, 20 Nov 1991, *Santos 184* (LPB, MO). **Rio de Janeiro:** Estrada da Itapuca, Via Guarativa, 13 Mar 1972, *Almeida 1347* (MO, RB). **Rondônia:** Vilhena, Vilhena arredores do aeroporto, -12.75, -60.166, 3 Jan 1979, *Silva 4122* (MO, NY). **Sergipe:** Santa Luzia do Itanhy, RPPN Mata do Crasto, Borda da mata, -11.3814, -37.4206, 23 Feb 2011, *Gomes 58* (NY). CARIBBEAN. **Trinidad:** Near Four Roads, 10.683333, -61.55, 33 m, 30 May 1924, *Riley 212* (BM, MO, NY). **Virgin Islands:** Tortola, Tortola. Government House Grounds, 18.37, -64.883333, 15 m, 5 Jan 1966, *D'Arcy 432* (MO). **Windward Islands:** St. Vincent, Kingstown, St. vincent, 13.133333, -61.216667, 4 Jan 1968, *Seibert 3058* (MO). COLOMBIA. **Antioquia:** Caucasia, Mpio. de Caucasia; along road to Nechi 17 km from Caucasia-Planeta Rica road, 7 km W of Hacienda Costarica. Disturbed roadside vegetation, 8.083, -75.15, 50 m, 22 Mar 1987, *Zarucchi 4921* (MO, NY). **Atlántico:** Juan Mina, Juanmina, 10.955, -74.891, 30 m, 18-19 Jan 1946, *Dugand 4071* (COL, NY). **Bolivar:** San Martín de Loba, Correg. “La Ribona”, 9, -74.083333, 70 m, 2 Mar 1993,

Ramirez 4505 (JAUM, MO). **Caqueta:** San Vicente del Caguan, Municipio San Vicente del Caguan: Sabanas del Yari, Vereda Alto de Morrocoy, Hato El Japon, 1.908, -74.025, 315 m, 30 Jan 1990, *Betancur 1681* (MO, NY). **Cesar:** Manaure Balcon del Cesar, Ca. 5 km W of Manaure on road to LaPaz, streamside moist forest remnant. Transect 1, 10.366, -73.133, 540 m, 26 Apr 1987, *Gentry 57132* (JBGP, MO). **Cordoba:** Ure, Corregimiento Ure, Cerromatoso, áreas aledañas a la explotación de Ferroniuel, 7.9, -75.55, 30–60 m, 24–25 Oct 1990, *Roldan 1458* (MO). **Guajira:** Sierra de San Antonio, Bosque de La Cueva, 11.0425, -73.4625, 350 m, 22 Aug 1986, *Hermes 2966* (MO, NY). **La Guajira:** Pueblo Viejo, Road from Mingueo to San Antonio de Pueblo Viejo, Serrania de Santa Marta S of Mingueo. Moist forest remnants, 11.166, -73.5, 200–400 m, 2 Jul 1984, *Gentry 47518* (MO). **Magdalena:** Santa Marta, Santa Marta, 11.247, -74.201, 166 m, 13 Jan 1898–1901, *Smith 739* (F, MO, NY, RB, UB). **Meta:** San Juan de Arama, Sabanas de San Juan de Arama, Rio Guejar, 3.346, -73.889, 500 m, 26 Jan 1951, *Idrobo-Muñoz 1327* (NY, U). **Narino:** Chucunes, Reserva Natural La Planada: 7 km above Chucunes (on road between Tuquerres and Ricaurte); along trail to Pialapí, 150–200 m past entrance to La Planada Field Station, 1.1, -77.883, 1700 m, 30 Sep 1970, *Thomas 12459* (MO, SCZ). **Santander:** Carare, Aeropuerto camino a Pto. Parra (Carare Opon Santander), 6.332, -73.336, 240 m, 10 Jun 1979, *Renteria 1525* (COL, MO, NY). **Sucre:** Coloso, Coloso to Finca Sirena, mostly along Quebrada El Salto, 9.496, -75.355, 300 m, 26 Oct 1989, *Gentry 68245* (MO, NY). COSTA RICA. **Puntarenas:** Golfo Dulce, R.F. Golfo Dulce; Península de Osa. El Ranchón. Los Mogos, 8.7527, -83.3833, 100 m, 12 May 1993, *Aguilar 1901* (CR, F, MO). FRENCH GUIANA. **Cayenne:** s.loc., 4.88333, -52.5, 11 Apr 2000, *Prévost 3844* (MO). GUYANA. **Rupununi:** Kaieteur Falls National Park, Potaro-Siparuni Region, Kaieteur Falls National Park. Open scrub with patches of forest. On very thin white or brown gravelly sand, 5.2, -59.483, 500 m, 2 Apr 1988, *Hahn 4081* (MO). PANAMA. **Canal Area:** Las Cumbres, Las Cumbres, Bethlemita, 9.083, -79.533, 15 Aug 1969, *Rivera 13* (GH, MO, PMA). **Chiriquí:** Burica Peninsula. Forest along quebradas and adjacent pastures; Quebrada Merida, 4 mi. (6.5 km) south of Puerto Armuelles, 8.21666, -82.88333, 0–100 m, 3 Mar 1973, *Liesner 395* (MO). **Colon:** Santa Rita Arriba, Santa Rita Ridge, 9.337, -79.78, 30 Dec 1971, *Dwyer 9410* (MO, NY). **Colón:** Portobelo, 9.55, -79.65, 30 Oct 1972, *Buitrago 9* (MO). **Darién:** Cerro Tacarcuna, South slope of Cerro Tacarcuna above Rio Pucuro base camp, 8.183, -77.283, 640–700 m, 29 Jan 1975, *Gentry 13999*

(MO). Isla Lagarto, small basaltic island in Golfo de San Miguel, 8.46666, -78.15, 2 Feb 1972, *Gentry 3979* (MO). **Panamá:** Chepo, 7 miles W of Chepo; mostly cleared area near highway, 9.166, -79.1, 1 Sep 1971, *Gentry 1639* (MO). **San Blás:** Isla Soskatupu, Isla Soskatupu, 8.97916, -77.775, 0–20 m, 9 Oct 1966, *Duke 8954* (MO).

PERU. **Loreto:** At mouth of Río Gueppi, tributary of Río Putumayo, northern most tip of Peru on border with Ecuador. Disturbed riverside vegetation, -0.11666, -75.25, 200 m, 19 May 1978, *Gentry 22087* (F, MO). VENEZUELA. **Amazonas:** Samariapo, Isla Caresita, 5 km NNW of Samariapo, 5.25, -67.8, 50 m, 3 Nov 1971, *Davidse 2870* (MO). **Anzoátegui:** Km 227 on Caracas-Barcelona highway, 16 km E of Boca de Uchire, 150 m, 4 Jul 1975, *Gentry 14834* (MO). **Apure:** Galeras del Cinaruco, Occasional along Rio Cinaruco for 29 km above Las Galeras de Cinaruco, 6.664444, -67.290278, 80–90 m, 24 Jan 1956, *Wurdack 41359* (NY, VEN). **Aragua:** Ocumare, About 5 km from Ocumare along road from Ocumare de la Costa to Maracay, 10.453, -67.768, 40 m, 7 Sep 1975, *Berry 1280* (MO, VEN). **Barinas:** Ticoporo, Ticoporo forest reserve, secondary forest, 8.25, -70.75, 370 m, 22 Jan 1964, *Breteler 3527* (F, MG, MO, NY, VEN). **Bolívar:** El Miamo, 2 kms from Hato de Nuria, E of Miamo, Altiplancie de Nuria, 7.617, -61.781, 400 m, 14 Jan 1961, *Steyermark 88414* (NY, UB, VEN). **Carabobo:** Rio Moron, Autonomo Mora, Cuenca hidrografica del Rio Moron, El Dique, 10.283, -68.166, 0–50 m, 20–21 Jul 1991, *Diaz 496* (MO, PORT). **Cojedes:** San Carlos, Laguna de la Culebra, near S. Carlos, 9.666, -68.6, 6 Apr 1925, *Pittier 11706* (NY). **Delta Amacuro:** El Palmar, ENE de El Palmar, 8.038, -61.906, 12 Jan 1965, *Marcano-Berti 550* (F, MO, NY, VEN).

Distrito Federal (Edo Vargas): Los Caracas, Rio Los Caracas, Los Caracas, 10.616, -66.566, 11 Feb 1973, *Croat 21611* (MO). **Falcon:** Buruica, Distrito Democracia, entre Cerro Pozo Azul y Cerro Moporal, 10.866, -70.3, 560–620 m, 1 Mar 1972, *Agostini 1014* (MO, NY, VEN). **Guarico:** Altigracia de Orituco, Valle de Guanape, Altigracia de Orituco, 9.9, -66.4, Oct 1966, *Aristeguieta 6456* (F, MO, NY, VEN).

Lara: Rio Claro, Rio Claro, 9.921, -69.355, Aug 1937, *Tamayo 292* (F, NY).

Miranda: Paparo, Paparo, 10.383, -65.983, 12 Mar 1923, *Pittier 11050* (NY, VEN).

Monagas: Temblador, Carretera de Barrancas a Temblador, puente sobre el Rio Uraoa. Vegetacion de Morichal, 9.016, -63.648, 50 m, 19 Apr 1973, *Agostini 1687* (F, MO, NY). **Portuguesa:** Guanare, Dtto. Guanare Cta. via Las Panelas 25 km W de Guanare, 9.066, -69.85, 250 m, 26 Jan 1984, *Aymard 2239* (MO, PORT). **Sucre:** Cristobal Colon, Puerto (same as Macuro), Cristobal Colon, 10.667, -61.934, Jan–Feb

1923, *Broadway 100* (NY). **Tachira:** El Pinal, Ayari, 15 km E of El Pinal, 7.49, -72.359, 300 m, 11 Nov 1980, *Maas 5234* (Mo, U). **Trujillo:** Valerita, 3 km NE of El Batatillo, 28 km NE of Valerita, 9.664, -70.56, 400 m, 30 Mar 1974, *Gentry 11024* (MO). **Yaracuy:** Yumare, Yumare, Colonia IAN, 10.602, -68.665, 10 Feb 1959, *Bernardi 7013* (NY). **Zulia:** Machiques, Dto. Perija, carretera a Calle Larga, 20 km sur de Machiques, 10.064, -72.545, 9 Mar 1978, *Bunting 6222* (MO, NY).

21. *Bignonia neouliginosa* L. G. Lohmann, *Ann. Missouri Bot. Gard.* 99(3): 421.

2014. Replaced name: *Phryganocydia uliginosa* Dugand, *Caldasia* 4(16): 59. 1946.

TYPE: Colombia. Atlántico: between Palmar de Varela and Ponedera, swamps of Río Magdalena, farm El Paraíso, 2--4 Aug. 1943, A. Dugand & R. Jaramillo 3491

(holotype: COL-14564 image!; isotype: US-1852300 image!).

Fig. 21: A–D

Description: Lianas. **Stems** solid, cylindrical, not winged, without lenticels (with lenticels), without interpetiolar gland fields, without interpetiolar ridge, without simple trichomes, sparsely to moderately lepidote; prophylls caducous, foliaceous, widely elliptic, ascending, sessile, symmetrical, 1.0 – 2.7 mm × 0.7 – 1.2 mm, without simple trichomes, densely lepidote, with many glands; bromeliad-like prophylls present. **Leaves** (1–)2-foliolate; petiole semi-cylindrical, 5.9 – 24.7 mm, without simple trichomes, moderately lepidote; petiolules caniculate, 5.2 – 11.1 mm, without simple trichomes, moderately lepidote; blades concolor, chartaceous, matte (laevigate), symmetrical, elliptic, rounded apically, rounded (cuneate) basely, 5.6 – 14.2 × 2.0 – 7.2 cm, adaxial surface without simple trichomes, not lepidote (very sparsely lepidote), with few glands at base and apex, abaxial surface without simple trichomes, very sparsely to sparsely lepidote, with few scattered glands dispersed, without domatia; venation pinnate, tertiary venations alternate percurrent; tendrils rarely present, simple, without simple trichomes, not lepidote, with glandular apex. **Inflorescences** compound dichasia, pauciflorae, corymbiform, terminal, without simple trichomes, sparsely lepidote, primary axis absent; bracts caducous, narrowly triangular, 0.9 – 2.0 × 0.3 – 0.7 mm, glabrous, without glands; pedicels 6.2 – 9.9 mm, without simple trichomes, sparsely lepidote. **Flowers** with calyx spathaceous, apiculate, plane, smooth, membranous, 19.9 – 28.8 × 6.0 – 10.0 mm wide at medium

height, without simple trichomes, sparsely lepidote, with many glands near and at apicule, apicules 2.3 – 4.6 mm; corolla purple outside, white inside, infundibuliform, dorso-ventrally flattened, membranous, (41.5 –) 58.7 – 86.6 mm, externally without simple trichomes, sparsely lepidote (only lobes sparsely lepidote), without glands, internally pubescent at base and lobes, sparsely lepidote on lobes, without glandular trichomes, tube (30.7 –) 40.8 – 58.8 × 2.8 – 4.4 mm wide at base and 10.6 – 22.4 mm wide at apex, lobes sub-circular, (8.6 –) 17.5 – 26.1 × (7.9 –) 17.5 – 26.2 mm; androecium didynamous, with stamens included, the largest (10.8 –) 15.6 – 16.9 mm, the shortest 9.3 – 14.5 mm, without simple trichomes, not lepidote, without glandular trichomes, thecae 3.2 – 4.2 mm, staminode 4.4 – 5.4 mm; gynoecium 29.3 – 31.3 mm, ovary cylindrical, smooth, without simple trichomes, densely lepidote, ovules in 2 series per locule, style moderately lepidote at basal portion; nectariferous disk reduced. **Fruits** flattened, narrowly oblong, 9.3 – 13.2 × 2.0 – 2.2 wide × 0.3 – 0.5 cm thick, valves woody, smooth, without ridges, without simple trichomes, densely lepidote, without glands. **Seeds** beige, slim, transversally oblong, symmetrical, 15.0 – 16.8 × 22.3 – 24.5 mm, seed body central, flattened, 0.8 – 1.2 mm thick, wings 2, opaque.

Distribution: This species is endemic to Magdalena Valley in **Colombia** (Atlántico, Cesar, Córdoba, Santander), exclusively found in swamps from 20 to 160 m (Fig. 20).

Phenology: Few specimens of *B. neouliginosa* have been collected, with flowering collections from March to August and December, and fruits in March, July and August.

Discussion: This species can be recognized by the elliptical and apically obtuse leaflets, pauciflorae inflorescences, short fruits (smaller than 13.2 cm) and by its restriction to swampy soils. It is very similar to *B. corymbosa*, which differs from *B. neouliginosa* by the larger, usually ovate and apically acute to acuminate leaflets, multiflorae inflorescences and longer fruits (> 20 cm).

Selected specimens: COLOMBIA. **Atlántico:** El Paraiso, El Paraiso, near Ponedera, 10.683, -74.733, 20 m, Apr 1939, *Dugand 1244* (MO); El Paraiso, 10.683, -74.733, 10 m, 1 Mar 1953, *Dugand 4605* (NY). Palmar de Varela, Palmar de Varela &

Ponedera, Rio Magdalena, 10.746, -74.755, 2–4 Aug 1943, *Dugand 3504* (COL, COTYPE); Between Palmar de Varela y Ponedera, Hac. El Paraiso, 10.746, -74.755, 10 m, 30 Jul 1951, *Dugand 4531* (COL, K, NY, US, VEN). **Bolivar**: La Raya, Municipio Achi, Corregimiento La Raya, 8.333, -74.5, 20–80 m, 6 Jul 1987, *Callejas 4370* (COL, MO, NY). Magangue, Magangue, 9.241, -74.753, 40–45 m, 18–19 Jan 1918, *Pennell 3932A* (NY). **Cesar**: Chiriguana, Savanna, Chiriguana, Magdalena Valley, 9.366, -73.606, 16 Jul 1924, *Allen 49* (MJC, MO). **Córdoba**: Ayapel, Ciénaga de Ayapel, La Ceja, 8.395556, -75.070556, 31 Mar 2004, *Rangel 13343* (COL). **Santander**: Barranca Bermeja, ca 5 km N of Barranca Bermeja on road to Puerto Wilches, 7.065, -73.868, 150 m, 24 Jul 1975, *Gentry 15364* (AAU, MO, NY).

22. *Bignonia phellosperma* (Hemsl.) L. G. Lohmann, Ann. Missouri Bot. Gard. 99(3): 421. 2014 = *Macfadyena phellosperma* Hemsl., Biol. Cent.-Amer., Bot. 2(12): 492. 1882 = *Phryganocydia phellosperma* (Hemsl.) Sandwith, Bull. Misc. Inform. Kew 1940(7): 302. 1940 [1941].

TYPE: Panama. Canal Zone [Coclé]: swamps of Río Grande, June 1861, *S. Hayes 81* (lectotype, designated here: K [K000449734] image!; isolectotypes: BM-630059!, K [K000449734] image!).

Fig. 22: A–B

Description: Lianas (shrubs). **Stems** solid, cylindrical, not winged, with lenticels, without interpetiolar gland fields, without interpetiolar ridge, without simple trichomes, sparsely lepidote (moderately lepidote); prophylls caducous, foliaceous, elliptic (cymbiform), spreading, sessile, asymmetrical, 0.8 – 3.0 mm × 0.6 – 1.7 mm, without simple trichomes, moderately lepidote, with many glands on adaxial surface; bromeliad-like prophylls present. **Leaves** 1–2-foliolate; petiole cylindrical to semi-cylindrical (caniculate), 12.8 – 61.5 mm, without simple trichomes, sparsely lepidote; petiolules caniculate, 8.9 – 36.6 mm, without simple trichomes, sparsely to moderately lepidote; blades concolor, chartaceous (sub-chartaceous), matte, slightly asymmetrical, ovate (elliptic), long acuminate apically, rounded to truncate (sub-cordate) basely, 6.8 – 14.9 × 4.0 – 9.1 cm, adaxial surface without simple trichomes, very sparsely to sparsely lepidote, with few glands at base and apex, abaxial surface without simple trichomes, sparsely lepidote, with few or no glands dispersed [over

blade], without domatia; venation pinnate, tertiary venations alternate percurrent; tendrils rarely present, simple, without simple trichomes, sparsely lepidote, with glandular apex. **Inflorescences** reduced thyrsi, 2-florae, corymbiform, terminal, without simple trichomes, sparsely lepidote, primary axis undeveloped; bracts caducous, narrowly elliptic, $4.3 - 7.7 \times 1.3 - 1.9$ mm, without simple trichomes, sparsely lepidote, with few glands; pedicels $3.5 - 7.1$ mm long, without simple trichomes, sparsely to moderately lepidote. **Flowers** with calyx spathaceous, 1-apiculate, plane, smooth, membranous, $16.0 - 26.4 \times 4.8 - 9.1$ mm wide at medium height, without simple trichomes, sparsely to moderately lepidote, with many glands near and at apicule, apicules $1.9 - 4.3$ mm; corolla purple outside, white inside, infundibuliform, dorso-ventrally flattened, membranous, $36.9 - 75.7$ mm, externally without simple trichomes (glabrescent), sparsely lepidote, without glands, internally pubescent at base and lobes (entirely pubescent), very sparsely to sparsely lepidote on lobes, without glandular trichomes, tube $23.7 - 49.7 \times 3.2 - 5.4$ mm wide at base and $10.3 - 18.7$ mm wide at apex, lobes sub-circular, $11.4 - 27.5 \times 7.4 - 25.3$ mm; androecium didynamous, with stamens included, the largest $10.3 - 17.6$ mm, the shortest $7.6 - 10.9$ mm, without simple trichomes, not lepidote, without glandular trichomes, thecae $2.9 - 3.7$ mm, staminode $1.4 - 6.3$ mm; gynoecium $24.5 - 27.3$ mm, ovary cylindrical (4-lobed), smooth, without glandular trichomes, densely lepidote, ovules in 2 series per locule, style sparsely lepidote at basal portion; nectariferous disk reduced. **Fruits** ellipsoid, ovate (elliptic), $5.3 - 7.5 \times 3.6 - 5.6$ wide $\times 0.5 - 1.8$ cm thick, valves woody, without ridges, smooth, without simple trichomes, densely lepidote, without glands. **Seeds** beige, corky, circular, symmetrical, $27.8 - 28.7 \times 27.1 - 31.1$ mm, seed body central, inflated, $0.8 - 1.2$ mm thick, wingless.

Distribution: *Bignonia phellosperma* is found mangroves in Pacific coast of **Colombia** (Chocó), **Costa Rica** (Guanacaste, Puntarenas) and **Panama** (Canal Area, Coclé, Darién, Panama) near sea level (Fig. 20).

Phenology: Flowering collections were obtained almost the whole year and fruiting collections from June to December.

Discussion: This species is characterized by the long acuminate leaflets apices, 2-florae inflorescences, spathaceous calices, ovate (elliptic) fruits and corky seeds. It is

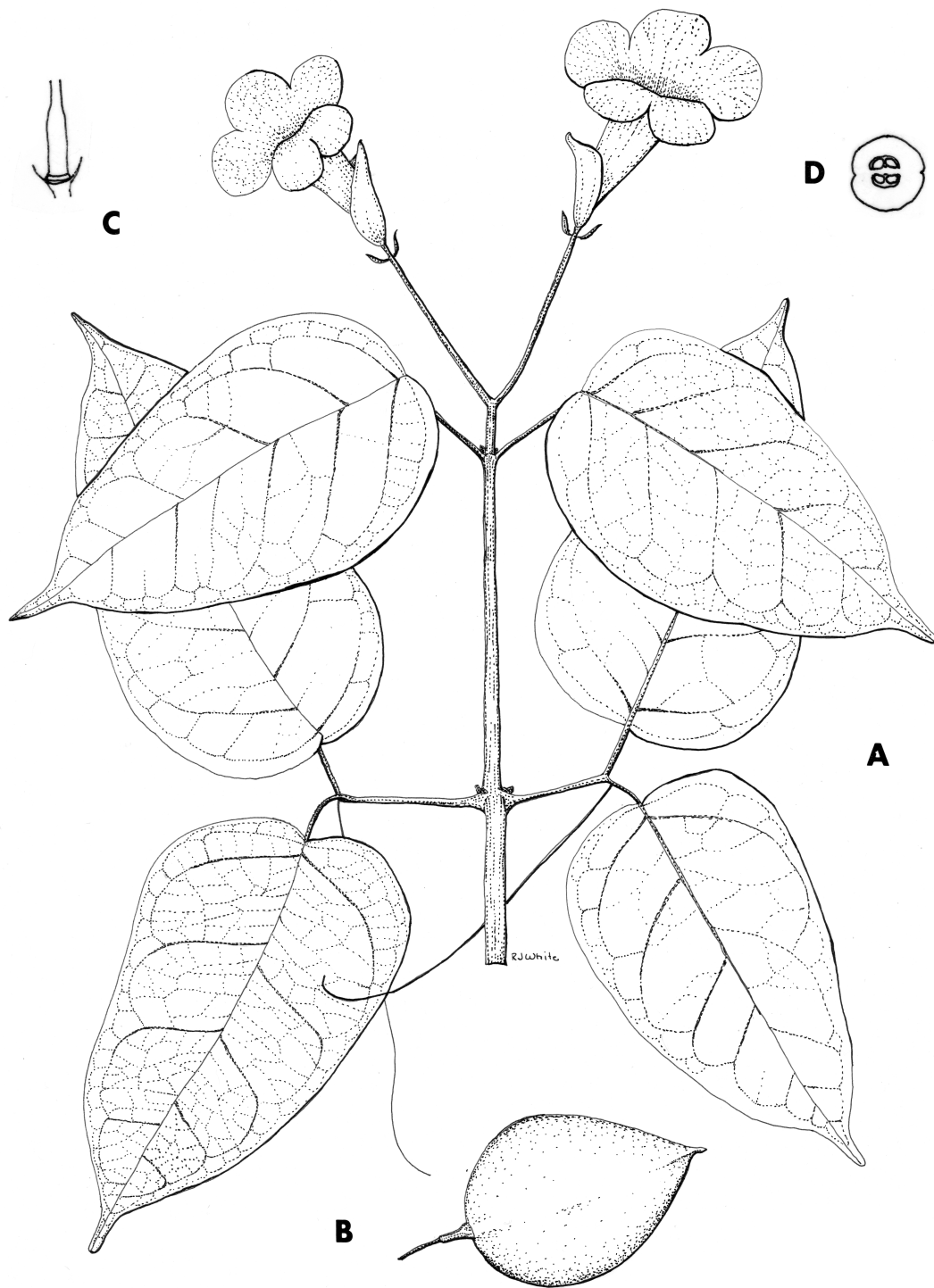


Figure 22. Morphology of *B. corymbosa* (Vent.) L.G. Lohmann and *B. phellosperma* (Hemsl.) L.G. Lohmann. **A–B** *B. phellosperma*: **A** Habit **B** Fruit; **C–D** *B. corymbosa*: **C** Ovary with undeveloped disk **D** Ovary cross-section. Illustrated from *Stern 59* (MO) [**A**], *Dwyer 1093* (MO) [**B**] and *Gentry 1450* (MO) [**C**]. From Gentry (1973: 906, fig. 26).

similar to *B. corymbosa*, but in this, the leaflet apices are rarely long acuminate, the inflorescences are multiflorae, the fruits are narrowly oblong to linear and seed are thin.

Bignonia phellosperma is one of the few hydrochoric species in the genus and, among these, presents the shortest distribution range, from Costa Rica to Northeastern Colombia.

In the protologue, Hesmley clearly designate the type as deposited at K. In this herbarium, however, two unnumbered sheets are found, one with leaves and flowers and the second with fruits. The first sheet is here selected as lectotype.

Selected specimens: COLOMBIA. **Chocó:** Mecana, Mangroves and adjacent beach. Mecana; Pacific coast N of Bahia Solano, 6.3, -77.383333, 0 m, 4 Mar 1983, *Gentry 40935* (MO). COSTA RICA. **Puntarenas:** Golfo Dulce, R.F. Golfo Dulce; Península de Osa. Rincón, junto a desembocadura del Río Rincón, 8.7, -83.486111, 10 m, 16 Oct 1993, *Aguilar 2578* (CR, MO). PANAMA. **Canal Area:** Miraflores, Miraflores Locks. Shrub in muddy flats below bridge at dam, 9.016, -79.516, Jul 1961, *Dwyer 1093* (MO). **Cocle:** Rio Grande, On banks of Rio Grande, C.Z, growing in mud, 8.416, -80.483, 21 Jun 1938, *Woodson 761* (A, MICH, MO, NY). **Darién:** Chepigana, Chepigana, 8.284, -78.041, *Duke 279* (MO). **Panamá:** San Carlos, Playa del Palma, near San Carlos Beach, 8.483, -79.95, 24 May 1967, *Lewis 1502* (GH, MO, UC, US).

I.V. *Bignonia* sect. *Potamoganos* (Sandwith) Zuntini, stat. et comb. nov. =

Potamoganos Sandwith, Receuil Trav. Bot. Néerl. 34: 220. 1937.

TYPE: *Bignonia microcalyx* G. Mey.

Description: Lianas. **Stems** cylindrical (tetragonal), not winged, without interpetiolar ridge; prophylls persistent, minute, connivent, sessile; bromeliad-like prophylls present or absent. **Leaves** 1–3-foliolate; blades matte, without leaf domatia; venation pinnate or actinodromous, tertiary venations alternate or opposite percurrent; tendrils with apex simple, bifid or trifid. **Inflorescences** racemes, axillary. **Flowers** with calyx cupular, truncate or 2-(3–5)-lobed, plane, smooth, sub-chartaceous to chartaceous, with or without glands; corolla purple, infundibuliform, with or without glands; androecium with stamens included; gynoecium with ovary cylindrical, smooth,

densely lepidote, ovules in 2 or 4 series per locule. **Fruits** flattened or cylindrical, linear or lanceolate, smooth, densely lepidote, with or without glands. **Seeds** slender, symmetrical, seed body central, flattened, wings 2, hyaline to translucent.

This section is characterized by presence of minute prophylls and axillary racemes. Although racemes can be found in other species, they are usually terminal.

Two species are included: *B. microcalyx* and *B. neoheterophylla*, distributed from Central America through Guiana Shields (Fig. 23).

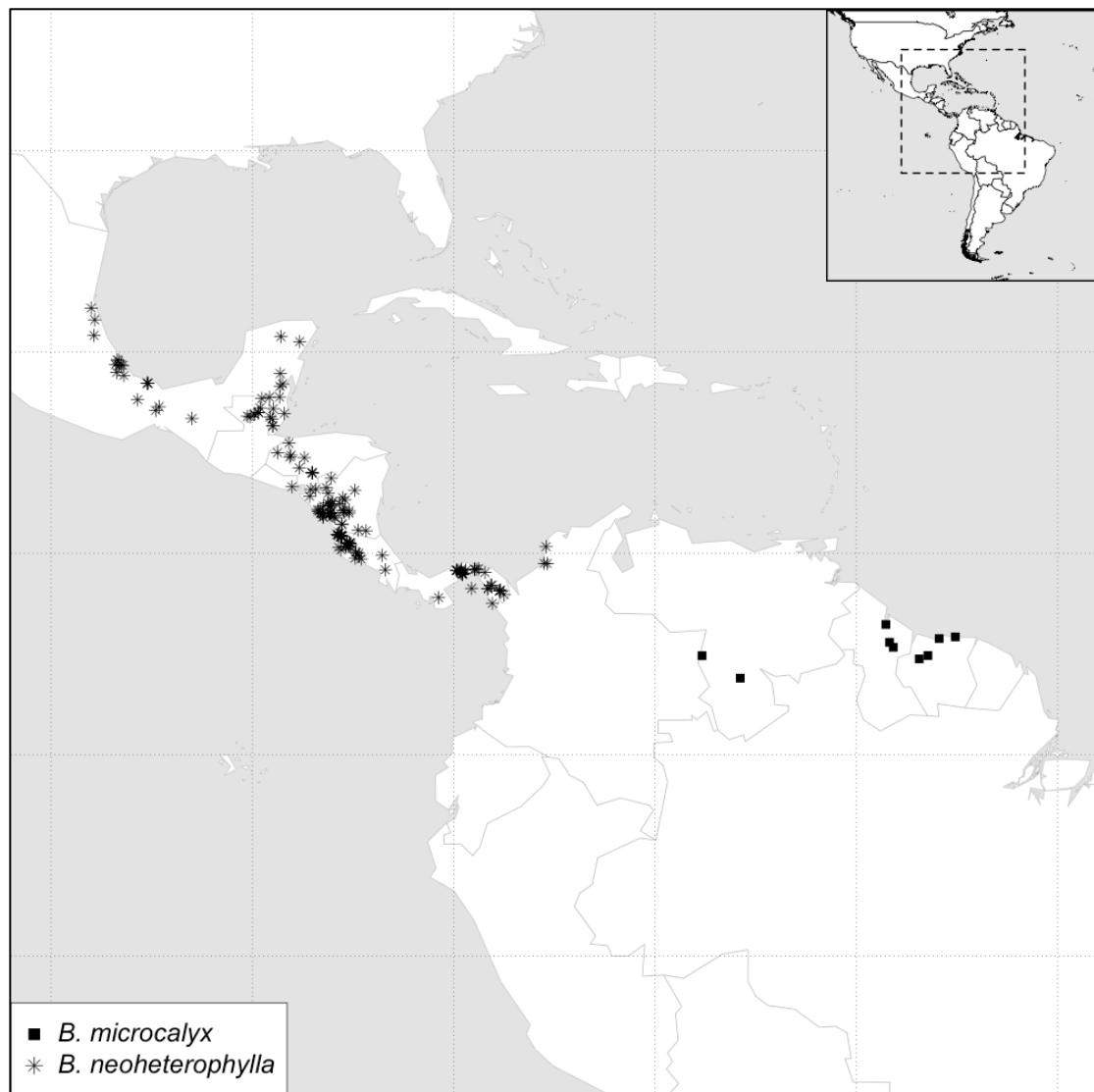


Figure 3. Distribution of *Bignonia* sect. *Potamoganos*. *B. microcalyx* G. Mey (solid square) and *B. neoheterophylla* L.G. Lohmann (asterisk)

23. *Bignonia microcalyx* G. Mey., Prim. Fl. Esseq. 211. 1818 = *Anemopaegma microcalyx* (G. Mey.) Bureau & K. Schum., Fl. Bras. 8(2): 134. 1896 = *Potamoganos microcalyx* (G. Mey.) Sandwith, Receuil Trav. Bot. Néerl. 34: 220. 1937, emend. Zuntini.

TYPE: Suriname, Sipaliwini, Along road from Zanderij to Kamp 52 in western Suriname, 181 km from Zanderij (10 km past (W of) bridge over Masonia Creek), 04°55'20"N 056°26'40"W, 50m, 5 February 2000, *R.J. Evans 3198* (neotype, designated here: MO-5946794!; isoneotypes: NY!, U)

Fig. 24

Description: Lianas. **Stems** solid, cylindrical (tetragonal), not winged, without lenticels, with interpetiolar gland fields (without gland field), without interpetiolar ridge (faint interpetiolar ridge), without simple trichomes, not lepidote; prophylls persistent, minute, semi-spherical, connivent, sessile, symmetrical, ca. 0.9 mm × 0.8 mm, without simple trichomes, not lepidote (lepidote), with or without glands; bromeliad-like prophylls absent. **Leaves** 2(–3)-foliolate; petiole cylindrical (semi-cylindrical), 33.0 – 72.5 mm, without simple trichomes, not lepidote (very sparsely lepidote); petiolules cylindrical or semi-cylindrical, 10.9 – 17.1 (–34.2) mm, without simple trichomes, not lepidote (very sparsely lepidote); blades concolor or slightly discolor, chartaceous (sub-coriaceous), matte, symmetrical, elliptic to widely elliptic, briefly acuminate to acuminate apically, rounded (cuneate) basely, 7.5 – 17.7 × 5.0 – 10.5 cm, adaxial surface without simple trichomes, not lepidote (very sparsely lepidote), with few scattered glands, abaxial surface without simple trichomes, sparsely lepidote, with few or no glands scattered, without domatia; venation pinnate, tertiary venation alternate percurrent; tendrils rarely present, simple, without simple trichomes, very sparsely lepidote, with trifid apex. **Inflorescences** simple racemes, pauciflorae, racemiform, axillary, without simple trichomes, moderately lepidote, primary axis 36.9 – 228.9 mm long; bracts caducous, linear to narrowly triangular, 0.9 – 1.3 mm × 0.2 – 0.6 mm, without simple trichomes, moderately lepidote, with glands; pedicels 11.5 – 22.5 mm, moderately lepidote, with few glands at apex. **Flowers** with calyx cupular, truncate, plane, smooth, sub-chartaceous, 2.8 – 3.8 × 4.1 – 6.9 mm wide at the apex, ciliate, moderately lepidote, with many glands near apex; corolla purple outside, white inside, infundibuliform, dorso-ventrally flattened, membranous, 56.4 – 85.4 mm, externally without simple trichomes, lobes moderately

lepidote, with few gland at lobes bases, without simple trichomes, lobes moderately lepidote, tube 35.1 – 53.9 × 2.3 – 4.7 mm wide at base and 10.7 – 20.5 mm wide at apex, lobes rounded to oblong, 14.0 – 24.0 × 14.8 – 26.9 mm; androecium didynamous, with stamens included, the largest 13.0 – 20.5 mm, the shortest 7.8 – 11.8 mm, without simple trichomes, not lepidote, without glandular trichomes, thecae 2.4 – 4.1 mm; staminode 2.7 – 4.5 mm; gynoecium (18.7–) 29.9 – 33.4 mm, ovary cylindrical, smooth, without simple trichomes, densely lepidote, ovules in 4 series per locule, style glabrous; nectariferous disk reduced. **Fruits** cylindrical, lanceolate, ca. 48.0 × 5.3 wide × 3.1 cm thick, valves petrous, without ridges, smooth, without simple trichomes, moderately lepidote, with few scattered glands. **Seeds** beige, slim, narrowly transversally oblong, symmetrical, 23.6 – 25.1 × 61.5 – 65.8 mm, seed body central, flattened, 1.2 – 1.4 mm thick, wings 2, opaque.

Distribution: This species can only be found in French Guiana, Guyana, Surinam and Venezuela, from sea level to 60 m (Fig. 23).

Phenology: Flowering collections are usually found between January and April, No collection with fruits has been identified so far.

Discussion: This species is characteristic by densely lepidote racemes, short calyces, and glands in stems, pedicels and corolla. The inflorescence structure and indument are shared with its sister species, *B. neoheterophylla*, but the calyx length (> 4.9 mm) and the gland fields (absent in *B. neoheterophylla*) allow the discrimination between these species. The glands in the stems can be found in other genera, like *Fridericia*, *Lundia* and *Tanaecium*, but in those, they are commonly placed between petioles and below the interpetiolar ridge (when present); in *B. microcalyx* these gland are often located above the ridge. These glands were distinctive in comparison to related genera (e.g. *Cydistia* and *Roentgenia*) and characterized the monotypic genus *Potamoganos* (Seibert 1948).

The glands described above are considered very distinctive in this species and their absence was the main reason for the exclusion of some specimens previously identified as *B. microcalyx*. All excluded specimens were sterile and the new determinations weren't possible. The removal of these collections led to recognition of a smaller distribution range, restricted to French Guiana, Guyana and Suriname, in

contrast with previous works, where its distribution also included Brazil and Venezuela (Hauk 2002, Funk et al. 2007, Lohmann and Taylor 2014).

The original description of *Anemopaegma microcalyx* didn't include fruits and seeds data and it was later emended by Sprague and Sandwith (1932: 86). Unfortunately, the emendation was based on a specimen that was posteriorly correctly identified as *Martinella obovata* (Kunth) Bureau & Schumann and therefore this emendation was discarded (Sandwith 1937). We here present a new emendation, based on Irwin 55572 (NY), providing the description of its fruit and seeds. The fruit is somewhat similar to *B. nocturna*, except by the acute apex (vs. rounded in *B. nocturna*) and it doesn't have remnants of the nectariferous disk as expected as a member of subgenus *Adiscae*. The seeds are like most *Bignonia*, with two opaque wings.

Bureau and Schumann (1896) provided the description for *Anemopaegma cupulatum* (Splitg.) Bureau & K. Schum. that matches the current circumscription and geographical range of *B. microcalyx*. Moreover, they mention the similarity between *A. cupulatum* and *Anemopaegma brachycalyx* [= *B. prieurii*], giving more support that the taxon described was indeed similar to *B. microcalyx*. However, they cited the protologue of *Bignonia cupulata* Splitg., what must be interpreted as a combination. The species, published by Splitgerber, differs from *B. microcalyx* by the multiflorae, sub-puberulous inflorescences and glabrous ovary, among other characters, and is considered a synonym of *Arrabidaea patellifera* (Schltdl.) Sandwith [= *Fridericia patellifera* (Schltdl.) L.G. Lohmann] (e.g. Gentry 1977a, 1982b). The combination of *B. cupulata* into *Anemopaegma* is valid (McNeill et al. 2012, Art. 41.1) and therefore *A. cupulatum* cannot be treated as synonym of *B. microcalyx*, as wrongly cited in Hauk (2002: 83). Furthermore, the description presented in Flora Brasiliensis later misled Pichon (1945) to transfer *A. cupulatum* to the new genus *Micropaegma* Pichon, along with *A. brachycalyx*, characterized by small calices and the tricolpate pollen (mostly pericolpate in *Anemopaegma*, Gentry & Tomb 1979). It is clear that *Micropaegma cupulatum* (Splitg.) Pichon would correspond to *B. microcalyx* but again cannot be treated as synonym of *B. microcalyx*.

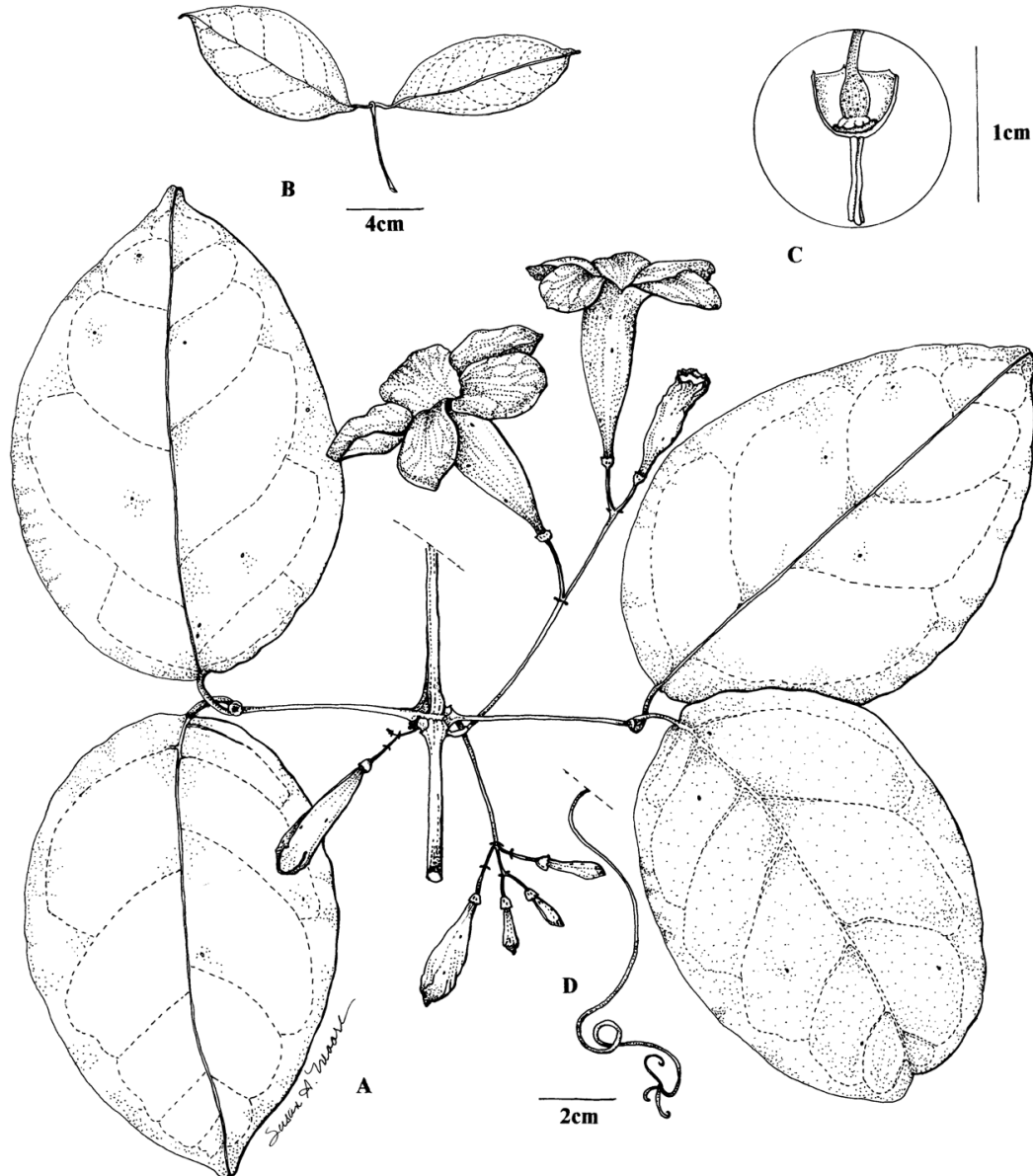


Figure 24. Morphology of *B. microcalyx* G. Mey. **A** Flowering branch **B** Leaf **C** Cut calyx and ovary **D** Tendril. Illustrated from *Miller 9418* (MO). From Hauk (2002: 84, fig. 2)

Selected specimens: GUYANA. **U. Demerara-Berbice.** Left bank of lower Kajarau Cr. (1 km above Macouria R on Essequibo R.), 6.466667, -58.533333, 5 m, 29 Apr 1993, *Henkel 1998* (MO, NY, US). **West Demerara:** Mabura Hill, Mabura Hill, 180 km SSE of Georgetown. Near township. Mixed forest on lateritic soil, 5.333, -58.166, 0–50 m, 23 Apr 1988, *Steege 357* (MO). Malali, Demerara River, 5.583, -58.35, 30 Oct 1922, *Cruz 2726* (CM, F, MO, US). SURINAME. **Saramacca:** Coppename River, Coppename River 3 km below base camp, 5.7666, -55.8833, 3 Feb 1965,

Florschütz 2734 (NY). Saramacca River, Fluv. Saramacca, prope Mt. Jabasigado, 5.85, -55.083333, Jan 1903, *Pulle 415* (MO). **Sipaliwini**: Blanche Marie Waterfall, Vicinity of Blanche Marie Waterfall on the Nickerie River, forest surrounding the Blanche Marie Guest House, 4.7561, -56.875, 60 m, 7 Feb 1998, *Miller 9418* (MO). Zanderij to Kamp, Along road from Zanderij to Kamp 52 in western Suriname, 181 km from Zanderij (10 km past (W of) bridge over Masonia Creek), 4.9222, -56.4444, 50 m, 5 Feb 1900, *Evans 3198* (MO). VENEZUELA. **Amazonas**: Huchamacari, Cerro, Cerro Huachamacari, Rio Cunucunuma, 3.8, -65.766, 400 m, 21 Dec 1950, *Maguire 29973* (NY, VEN). Rio Cuao, Rio Cuao, Rio Orinoco, 4.9167, -67.666, 125 m, 19 Jan 1949, *Maguire 28436* (F, NY, US).

24. *Bignonia neoheterophylla* L. G. Lohmann, Ann. Missouri Bot. Gard. 99(3): 420. 2014. Replaced name: *Cydista heterophylla* Seibert, Publ. Carnegie Inst. Wash. 522: 417, Plate 6. 1940.

TYPE: Mexico. Yucatán: near Xocenpich, May – Aug 1938, *C.L. Lundell & A.A. Lundell 7350* (holotype: MICH-1115829 image!, MICH as un-numbered photo at MO-1244826!; isotypes: A [A00091980] image!, F-1309020!, LL [LL00373021] image!, S S-G-1822 image!, US-1840031 image!).

Fig. 25

Bignonia lepidota Seem. Bot. Voy. Herald: 179. 1854, hom. illeg., *non Bignonia lepidota* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 139.

TYPE: Panama. Isla de Iguana, May 1947, *B.C. Seemaaan 601* (lectotype, designated here: K [K000449732] image!, isolectotype: BM [BM000992365] image!)

Description: Lianas. **Stems** solid, cylindrical (sub-tetragonal), not winged, with lenticels, without interpetiolar gland fields, without interpetiolar ridge, without simple trichomes, sparsely to moderately lepidote (densely lepidote when immature); prophylls persistent, subulate, cymbiform, connivent, sessile, symmetrical, 1.7 – 2.2 mm × 0.6 – 1.0 mm, without simple trichomes, densely lepidote, without glands; bromeliad-like prophylls present. **Leaves** 1–2(–3)-foliolate; petiole cylindrical (semi-cylindrical), 18.1 – 48.9 mm, without simple trichomes, sparsely to moderately lepidote; petiolules caniculate, 13.9 – 25.8 mm, without simple trichomes, sparsely

lepidote (moderately lepidote); blades discolor, chartaceous, matte, symmetrical (slightly asymmetrical), ovate (elliptic), obtuse (acuminate) apically, truncate (rounded) basely, $7.2 - 11.8 (-17.0) \times 4.1 - 9.4$ cm, adaxial surface without simple trichomes, very sparsely lepidote (sparsely lepidote), without glands (few scattered glands when immature), abaxial surface without simple trichomes, sparsely lepidote (very sparsely to moderately lepidote), with many glands at base, without domatia; venation actinodromous (sub-actinodromous), tertiary venations opposite percurrent (mixed opposite-alternate); tendrils rarely present, simple, without simple trichomes, very sparsely lepidote, with simple apex. **Inflorescences** raceme, pauciflorae, racemiform, axillary, without simple trichomes, densely lepidote, primary axis $6.1 - 92.1 (-14.0)$ mm long; bracts caducous, triangular or circular, $1.1 - 1.7 \times 0.7 - 1.5$ mm, without simple trichomes, densely lepidote, without glands; pedicels $6.0 - 18.5$ mm, without simple trichomes, densely lepidote, without glands. **Flowers** with calyx cupular, 2(-3-5)-lobed, plane, smooth (with few protuberances), chartaceous, $4.9 - 7.0 \times 4.9 - 7.2$ mm wide at apex, without simple trichomes, densely lepidote, without glands (with few clustered glands), lobes $0.9 - 2.5$ mm; corolla purple outside, white inside, infundibuliform, dorso-ventrally flattened, membranous, $40.5 - 86.1$ mm, externally without simple trichomes (glabrescent at lobes), sparsely lepidote, without glands, internally pubescent at base and lobes, sparsely lepidote (very sparsely lepidote), without glandular trichomes, tube $24.4 - 55.3 \times 2.5 - 4.2$ mm wide at base and $8.2 - 17.2$ mm wide at apex, lobes spatulate, $9.7 - 31.3 \times 9.9 - 27.5$ mm; androecium didynamous, with stamens included, the largest $15.2 - 18.9$ mm, the shortest $10.3 - 13.9$ mm, glabrescent at base, not lepidote, without glandular trichomes, thecae $3.1 - 3.9$ mm, staminode $3.8 - 7.0$ mm; gynoecium $22.7 - 33.7$ mm, ovary cylindrical, smooth, densely lepidote, ovules in 2 series per locule, style sparsely lepidote at basal portion; nectariferous disk reduced. **Fruits** flattened, linear, $20.0 - 48.5 \times (0.8 -) 1.2 - 2.6$ wide $\times 0.4 - 0.9$ cm thick, valves woody, with 2 longitudinal ridges, smooth, without simple trichomes, densely lepidote, without glands. **Seeds** beige, slim, narrowly transversally oblong, symmetrical, $9.3 - 16.5 \times 35.9 - 72.3$ mm, seed body central, flattened, $0.7 - 1.5$ mm thick, wings 2, hyaline to translucent.

Distribution: This species occurs from mangroves and riparian forest to semi-deciduous forests, in **Belize** (Cayo, Orange Walk, Toledo), **Costa Rica** (Alajuela,

Guanacaste, Puntarenas), **El Salvador** (La Union), **Guatemala** (Petén), **Honduras** (Francisco Morazán, Santa Bárbara), **Mexico** (Chiapas, Jalisco, Oaxaca, Quintana Roo, Veracruz, Yucatan), **Nicaragua** (Boaco, Chinandega, Chontales, Estelí, Granada, Leon, Managua, Masaya, Matagalpa, Nueva Segovia, Río San Juan, Rivas, Zelaya) and **Panama** (Canal Area, Colon, Darién, Herrera, Panama) from sea level to 300m (Fig. 23).

Phenology: Flowers and fruits throughout the year, both being more abundant between May and June.

Discussion: This species is distinctive by the usually leafless flowering plants, densely lepidote indument that covers young stems and leaves, inflorescences and calyces. Additionally, axillary racemes, usually 2-lobed calyces (often with few glands) and fruits with 2 longitudinal ridges are characteristics of *B. neoheterophylla*. It is similar to its sister species, *B. microcalyx*, but can easily be distinguished as explained in the discussion of the latter.

The name *Bignonia lepidota* Seem. is a later homonym of *Bignonia lepidota* Kunth [\equiv *Tabebuia lepidota* (Kunth) Britton] and hence illegitimate. However, since it was validly published, it must have a designated type to fix its identity. Among the 4 syntypes cited, we choose as lectotype Seemann 601 (at K) since it matches the description, can be unequivocally identified, has duplicates and is not an admixture.

Selected specimens: BELIZE. **Belize:** Stann Creek Valley, Stann Creek Railway, 16.95, -88.416667, 33 m, 26 May 1929, *Schipp 224* (F, MICH, MO, NY). **Cayo:** Caracol, 4.5 km before Caracol, 16.7666, -89.1166, 23 May 1991, *Balick 3152* (MO, NY). **Orange Walk:** Indian Church, 17.76666, -88.65, Jun 1976, *Arnason 17341* (MO). **Toledo:** Columbia River Forest Reserve, Trail from Columbia Forest Station to Esperanza, 2-4 miles W of San Jose road, 16.333333, -88.983333, 200–366 m, 13 Jun 1973, *Gentry 8192* (MO). COLOMBIA. **Bolivar:** Turbaco, La Cantera de Cimaco, near Cartagena, 10.332, -75.411, 100 m, 2 Jan 1993, *Gentry 78483* (MO). **Sucre:** Coloso, Coloso, Estacion de Primates, forest on limestone. Transect 2, 9.496, -75.355, 300 m, 25 Oct 1989, *Gentry 68146* (MO). COSTA RICA. **Alajuela:** Caldera, Between Caldera and Orotina near Sitio Huacas, 9.9, -83.55, 150 m, 8 Jul 1990, *Gentry 71439* (MO). **Guanacaste:** P.N. Palo Verde. Valle del Tempisque. Estación

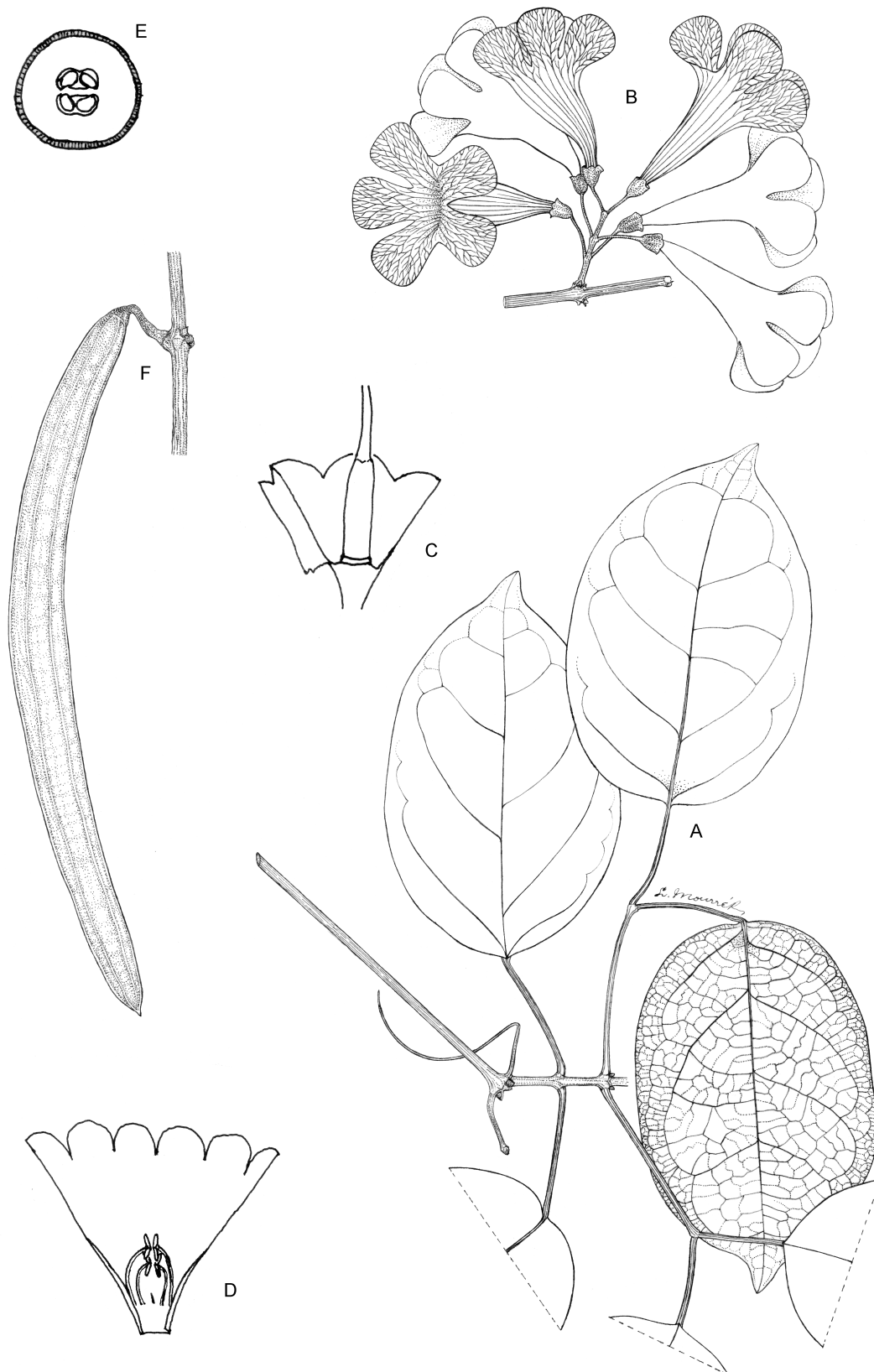


Figure 25. Morphology of *B. neoheterophylla* L.G. Lohmann. **A** Inflorescence **B** Ovary cross-section **C** Fruit **D** Open calyx and ovary **E** Sterile Branch **F** Open corolla. Illustrated from *Gentry 4967* (MO) [**ABF**] and *Gentry 4088* (MO) [**C-E**]. From Gentry (1973: 841, fig. 10).

Palo Verde, 10.35, -85.35, 10 m, 30 Nov 1995, *Chavarría 1368* (MO). **Puntarenas:** Río Grande de Tárcoles, Punta Loros y alrededores, 9.851389, -84.7, 20 m, 25 Mar 1993, *Hammel 18855* (F, INB). EL SALVADOR. **La Unión:** Lagun de Olomega, Carretera a la Lagun de Olomega. Bejuco de flores rojo-moradas, 13.311111, -88.026667, 3 May 1957, *Lagos 625* (MO). GUATEMALA. **Petén:** El Remate, El Remate, km 12, Santa Elena, 17, -89.7, 22 May 1971, *Tun 1764* (F, NY).

HONDURAS. **Choluteca:** San Francisco, 5 km NW of San Francisco, 13.180833, -87.098333, 800 m, 2 Jun 1965, *Lent 598* (F, MO). **Comayagua:** Humuya, Union del rio Yure con rio Humuya, 14.25, -87.6666666999997, 200 m, 22 Nov 1980, *Nelson 6083* (MO, TEFH). **Copán:** San Nicolas, Entre San Nicolas y Trinidad, carretera Santa Rosa de Copan, 15, -88.75, 1000 m, 30 Mar 1963, *Molina 11725* (EAP, F, NY). **Cortés:** Entre Cofradía y Montaña Cusuco, 15.47194, -88.17861, 200–1300 m, 26 May 1956, *Molina 7302* (F, MO). **Francisco Morazán:** Open fields near Pedregal, 13.99861, -87.04055, 850 m, 14 Jun 1947, *Molina 115* (F, MO). **Santa Bárbara:** Lago Yojoa, 16 km W of the southern end of Lago Yojoa along new highway to Santa Bárbara. Forested hills with *Pinus caribbea* and broad-leaved trees along stream, 14.7833, -88.1333, 550 m, 11 May 1991, *Davidse 34302* (MO). **Yoro:** Entre Yoro y Morazan, 700 m, 1 Jan 1904, *Molina 6925* (F, MO). MEXICO. **Chiapas:** Chiapa de Corzo, Chiapa de Corzo, 5.6 mi E of Chiapa de Corzo, 16.7, -93, 833 m, 7 Apr 1965, *Breedlove 9559* (F). **Jalisco:** Puerto Vallarta, Puerto Vallarta, 20.616, -105.25, 16 m, 1 Sep 1979, *Croat 45406* (MO). **Nayarit:** Chacala, Km 6.5, camino de terraceria de Las Vargas-Chacala, 21.166, -105.233, 16 Jun 1987, *Tellez 10369* (MO). **Oaxaca:** Esmeralda, Mpio. Matias Romero, 8 km S de Esmeralda, 17.1, -94.8, 150 m, 21 Apr 1985, *Wendt 4809* (MO, NY). **Quintana Roo:** Coba, 7 km N de Coba, hacia Nuevo Xcan, 20.516, -87.65, 11 Jun 1980, *Tellez 2518* (MEXU, MO, NY). **Veracruz:** San Andres Tuxtla, San Andres Tuxtla, Laguna Encantada, 6 km al norte de San Andres Tuxtla, 18.45, -95.216, 24 Jan 1973, *Calzada 978* (F, MO). **Yucatan:** Xocenpich, Near Xocenpich, in young legume thicket, 20.766, -88.583, May–Aug 1938, *Lundell 7350* (MO(photo)). NICARAGUA. **Boaco:** Boaco, Carretera 7 between Boaca cutoff & Acoyapa, 12.466667, -85.666667, 100–250 m, 18 Mar 1961, *Bunting 729* (F, NY). **Chinandega:** Puerto Morazan, Camino de Puerto Morazán a Tonalá; Manglares y sabanas inundadas, 12.8333, -87.15, 30–40 m, 7 Jun 1983, *Sandino 4363* (MO). **Chontales:** Puente Lovago, ca 5.3 km W of Puente Lóvago, Km 160; ca. 12 |100'N, 85 |112'W, elev. 150-170 m; steep rocky barranca (cliff), 12, -85.2, 150–170 m, 7 Jun

1981, *Henrich 181* (MO). **Esteli:** Mechapa, Mechapa, 3 km al N de la Trinidad sobre la carretera Panamericana; 12 |159'N, 86 |114'W, elev. aprox. 700 m, 12.9833, -86.2333, 700 m, 24 Oct 1983, *Moreno 22435* (MO). **Granada:** Volcán Mombacho, Volcán Mombacho, La Calera, camino a Cutirre, 11.85, -85.95, 300–330 m, 11 May 1981, *Moreno 8458* (MO). **Leon:** Quebrada Las Ruedas, Slope and ridge immediately W of Quebrada Las Ruedas, N of road, NW of El Transito; ridge of broken shale and thin soil, open jicaro savanna, slope with deeper soil and taller forest, 12.0833, -86.7166, 15–30 m, 13 May 1981, *Stevens 20138* (MO). **Managua:** San Cayetano, Along Hwy. 10 between San Cayetano and Villa El Carmen, 11.9499, -86.5083, 100–130 m, 11 May 1980, *Stevens 17142* (MO). **Masaya:** Parque Nacional Volcán Masaya, 1 km E of Volcán Masaya; dry scrub forest on lava flow, 11.9833, -86.1333, 300 m, 14 Feb 1978, *Neill 3184* (MO). **Matagalpa:** Muy Muy, Ranchería, 11 km al NE de Muy muy; 12 |146'N, 85 |131'W, elev. aprox. 280 m, 12.7666, -85.5166, 280 m, 20 Aug 1984, *Moreno 24480* (MO). **Nueva Segovia:** El Jicaro, El Jicaro, “Casas Viejas”; 13 |144'N, 86 |105'W, elev. aprox. 600 m, 13.7333, -86.0833, 600 m, 24 Dec 1981, *Moreno 13505* (MO). **Rivas:** Isla Ometepe, Isla Ometepe, Volcán Maderas, Mérida. Bosque seco tropical matorraloso, vegetación secundaria, abundante en *Ficus*, *Gliricidia*, *Pithecellobium*, *Cordia*, 11.45, -85.55, 200–280 m, 27 Apr 1984, *Robleto 397B* (MO). **Río San Juan:** El Castillo, Municipio El Castillo, Comunidad El Monico, 11.12083, -84.35111, 100 m, 8 Jun 2005, *Guido 4532* (HULE, MO). **Zelaya:** Kurinwacito, Kurinwacito; 13 |108'N, 84 |155'W, elev. aprox. 80 m, 13.1333, -84.9166, 80 m, 30 Apr 1984, *Moreno 23975* (MO). PANAMA. **Canal Area:** Miraflores Locks, Victoria Fill, near Miraflores Locks, 8.993, -79.582, 2 Apr 1939, *Allen 1756* (MO). **Colón:** Madden Forest, Madden Forest. Nitrogen vouchers, 9.133, -79.611, 22 Sep 1971, *Gentry 1927* (MO). **Darien:** Pavarando, Cerro Pavarando to top of Cerro Derumba, 7.518, -78.077, 1000 m, 10 Feb 1972, *Gentry 4206* (MO). **Herrera:** Las Minas, 12.5 mile E of Las Minas, 7.8, -80.75, 13 Dec 1971, *Gentry 3143* (MO). **Panamá:** El Llano, 1 mi E of El Llano, 9.212, -78.964, 1 May 1971, *Croat 14499* (MO).

I.VI. Bignonia sect. Roentgenia (Urb.) Zuntini, stat. et comb. nov. = *Roentgenia* Urb., Ber. Deutsch. Bot. Ges. 34: 747. 1916.

TYPE: *Bignonia bracteomana* (K. Schum. ex Sprague) L. G. Lohmann

Description: Lianas. **Stems** cylindrical to tetragonal, not winged, with interpetiolar ridge; prophylls persistent or caducous, falcate, ascending, stipitate, with or without glands; bromeliad-like prophylls absent. **Leaves** 2-foliolate; blades matte, with pocket and trichomes tufts domatia; venation pinnate, tertiary venations opposite percurrent; tendrils with apex bifid or trifid. **Inflorescences** thyrsi with lateral dichasia sessile, terminal or lateral. **Flowers** with calyx cupular, truncate (2-lobed or 5-apiculate), plane (ribbed), verrucose, sub-chartaceous, with glands; corolla white or purple, infundibuliform, without glands; androecium with stamens included; gynoecium with ovary cylindrical (tetragonal), smooth, densely lepidote, ovules in 2 series per locule. **Fruits** flattened, linear (narrowly oblong), finely verrucose, densely lepidote, without glands. **Seeds** slender, symmetrical, seed body central, flattened or lenticulate, wings 2, opaque.

Bignonia sect. Roentgenia is characterized by tendril apically trifid, tertiary venation opposite percurrent (or mixed), thyrsi with lateral simple and sessile dichasia and the 4-colpate pollen. Additionally, herbarium specimens tend to dry light brownish.

Two species are included in this section: *B. bracteomana* and *B. sordida*, distinguishable by the floral bracts (persistent vs. caducous) and indument (mostly without simple trichomes vs. minutely villous). The species are distributed in Amazonia and Guiana Shield (Fig. 26).

25. *Bignonia bracteomana* (K. Schum. ex Sprague) L. G. Lohmann, Ann. Missouri Bot. Gard. 99(3): 417. 2014 = *Cydista bracteomana* K. Schum. ex Sprague, Verh. Bot. Vereins Prov. Brandenburg 50: 121. 1908 [1909] = *Roentgenia bracteomana* (K. Schum. ex Sprague) Urb., Ber. Deutsch. Bot. Ges. 34: 748. 1916.

TYPE: Brazil. Amazonas: Victoria, Juruá River, May 1901, E. Ule 5497 (holotype: B†; lectotype, designated here, HBG-522503; isoelectotypes: L-0003407!, MG-5444!).

Fig. 27: F–G

Description: Lianas (shrubs). **Stems** solid, cylindrical to tetragonal, not winged, with lenticels, without interpetiolar gland fields, with interpetiolar ridge, without simple trichomes (glabrescent), moderately lepidote; prophylls persistent (upper part

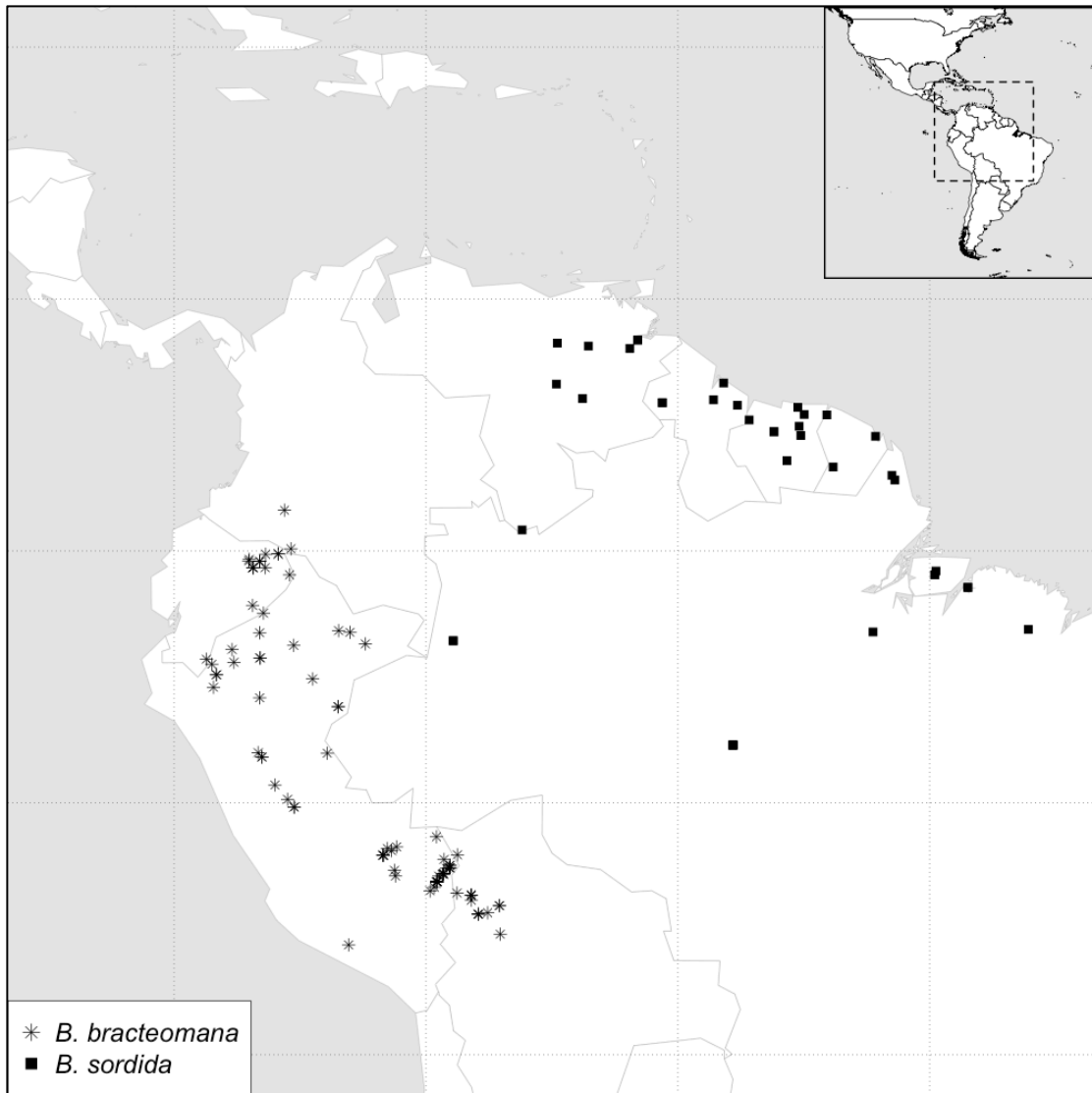


Figure 26. Distribution of *Bignonia* sect. *Roentgenia*. *B. bracteomana* (K. Schum. ex Sprague) L. G. Lohmann (asterisk) and *B. sordida* (Bureau & K. Schum.) L.G. Lohmann (solid square)

deciduous), foliaceous, broadly falcate (oblate or spatulate), ascending, stipitate, asymmetrical (symmetrical), 5.7 – 10.4 (– 20.4) × 3.0 – 9.8 (– 14.7) mm, without simple trichomes, moderately lepidote, with many glands; bromeliad-like prophylls absent. **Leaves** 2-foliolate; petiole semi-cylindrical, 6.7 – 32.0 (– 55.0) mm, without simple trichomes (puberulous), moderately to densely lepidote (sparsely lepidote); petiolules cylindrical or caniculate, 8.1 – 37.4 (– 46.0) mm, without simple trichomes (puberulent), moderately lepidote (sparsely lepidote); blades concolor (slightly discolor), chartaceous (membranous), matte, symmetrical, ovate to elliptic, acute (acuminate) apically, rounded basely, 11.2 – 24.5 (– 30.0) × 4.7 – 11.0 cm, adaxial surface without simple trichomes, sparsely lepidote, without glands (few scattered

glands), abaxial surface without simple trichomes, sparsely to moderately lepidote, with few to many scattered glands [few ~ 6 to many ~40], with pocket and trichomes tufts domatia on axils of midvein; venation pinnate, tertiary venations mostly opposite percurrent; tendrils rarely present, simple, without simple trichomes, not lepidote or sparsely lepidote, with briefly 2–3-fid apex. **Inflorescences** thyrsi, with lateral dichasia simple and sessile, multiflorae, racemiform, terminal and lateral, without simple trichomes, moderately lepidote (densely lepidote at nodes), primary axis 39.8–129.0 mm long; bracts persistent, cymbiform (3-lobed), 6.2–15.4 × 1.0–2.2 mm, without simple trichomes, moderately lepidote, with or without glands; pedicels 4.4–8.7 (–11.0) mm long, without simple trichomes, lepidote (sparsely lepidote), without glands. **Flowers** with calyx cupular, truncate or irregularly undulate to shallowly lobed (2-lobed), plane (ribbed), verrucose, sub-chartaceous, 5.7–9.3 × 4.2–7.3 mm wide at the apex, without simple trichomes, lepidote to densely lepidote (sparsely lepidote), with many glands (few glands), lobes when present 1.0–3.5 mm; corolla white (pinkish) outside, purple (yellow) inside, infundibuliform, dorso-ventrally flattened, membranous, 39.5–69.9 mm, externally without simple trichomes, sparsely lepidote (moderately lepidote at base), without glands, internally without simple trichomes, sparsely lepidote, with glandular stipitate trichomes at base and lobes, tube 28.2–44.8 × 2.1–3.6 mm wide at base and 9.7–17.5 mm wide at apex, lobes sub-circular or oblong, 7.9–19.7 × 7.1–16.4 mm; androecium didynamous, with stamens included, the largest 15.0–24.1 mm, the shortest 8.3–13.5 mm, without simple trichomes, not lepidote, with stipitate glandular trichomes at base, thecae 2.9–4.1 mm, staminode 3.5–4.0 mm; gynoecium (13.4–) 26.4–38.0 mm, ovary cylindrical (tetragonal), smooth, without simple trichomes, densely lepidote, ovules in 2 series per locule, style sparsely lepidote at base; nectariferous disk reduced. **Fruits** flattened, linear, 32.0–69.0 × 2.0–2.6 wide × 0.5–1.0 thick cm wide, valves woody, without ridges, finely verrucose, without simple trichomes, not lepidote to sparsely lepidote (densely lepidote when immature), without glands. **Seeds** brown, slim, narrowly transversally oblong, symmetrical, 14.0–22.4 × 45.0–81.8 mm, seed body central, flattened, 0.4–0.6 mm thick, wings 2, opaque.

Distribution: *Bignonia bracteomana* is commonly found in riparian forest on non-flooded soils in **Bolivia** (Beni and La Paz), **Colombia** (Caquetá), Ecuador (Napó, Pastaza, Sucumbíos and Zamora-Chinchipec) and **Peru** (Amazonas, Huánuco, Loreto,

Madre de Dios, Puno, San Martín and Ucayali), from 150 to 400 m (Fig. 26).

Phenology: Flowering specimens have been collected throughout the year, but more abundantly in January, February and October. Fruits are recorded from February to October.

Discussion: This species can be distinguished by its combination of simple tendrils with the apex orthogonally 2-3-fid, broadly falcate prophylls bearing many glands, glandular trichomes on the filaments, and distinctive inflorescence structure: the inflorescence is racemiform with a well developed primary axis bearing sessile lateral dichasia that are subtended by large bracts. Some of characters are found in *B. sordida*, which differs in its caducous and smaller bracts (< 8 mm long). When no flowers are present, the indument on the petioles and petiolules can be used to separate these species: these are glabrous to rarely puberulous in *B. bracteomana* vs. minutely villous in *B. sordida*.

Sprague described this species, attributing it to Karl Schumann, using the bracts as diagnostic feature from the other species of *Cydista*, although he stated his uncertainty about its generic placement. Later, Urban considered this very different from the other species because of its bracts, and separated it in its own genus, *Roentgenia*, which was additionally characterized by non-pericolpate pollen, bracts, eglandular anthers, 2-3-fid tendrils and fleshy calyx. These two genera were recognized as related by Gentry (1974a), but their circumscription hasn't change until Lohmann & Taylor (2014).

The holotype, deposited in B, was supposedly destroyed and thus we designate here the duplicate deposited at HBG as lectotype. Besides been the better-preserved material, this specimen is likely to be seen by the author, Karl Schumann.

Selected specimens: BOLIVIA. **Beni:** Yucumo-Rurrenabaque, Km 35 carretera Yucumo-Rurrenabaque, Colegio Técnico Agropecuario Río Colorado. Bosque tropical pluvial, zona húmeda pero no inundable, terreno plano, bosque primario con frecuentes perturbios naturales. Especímenes preservados con alcohol, -14.083333, -67.083333, 230 m, 28 Feb 1990, *Smith 14066* (LPB, MO). **La Paz:** Río Satariapo, Río

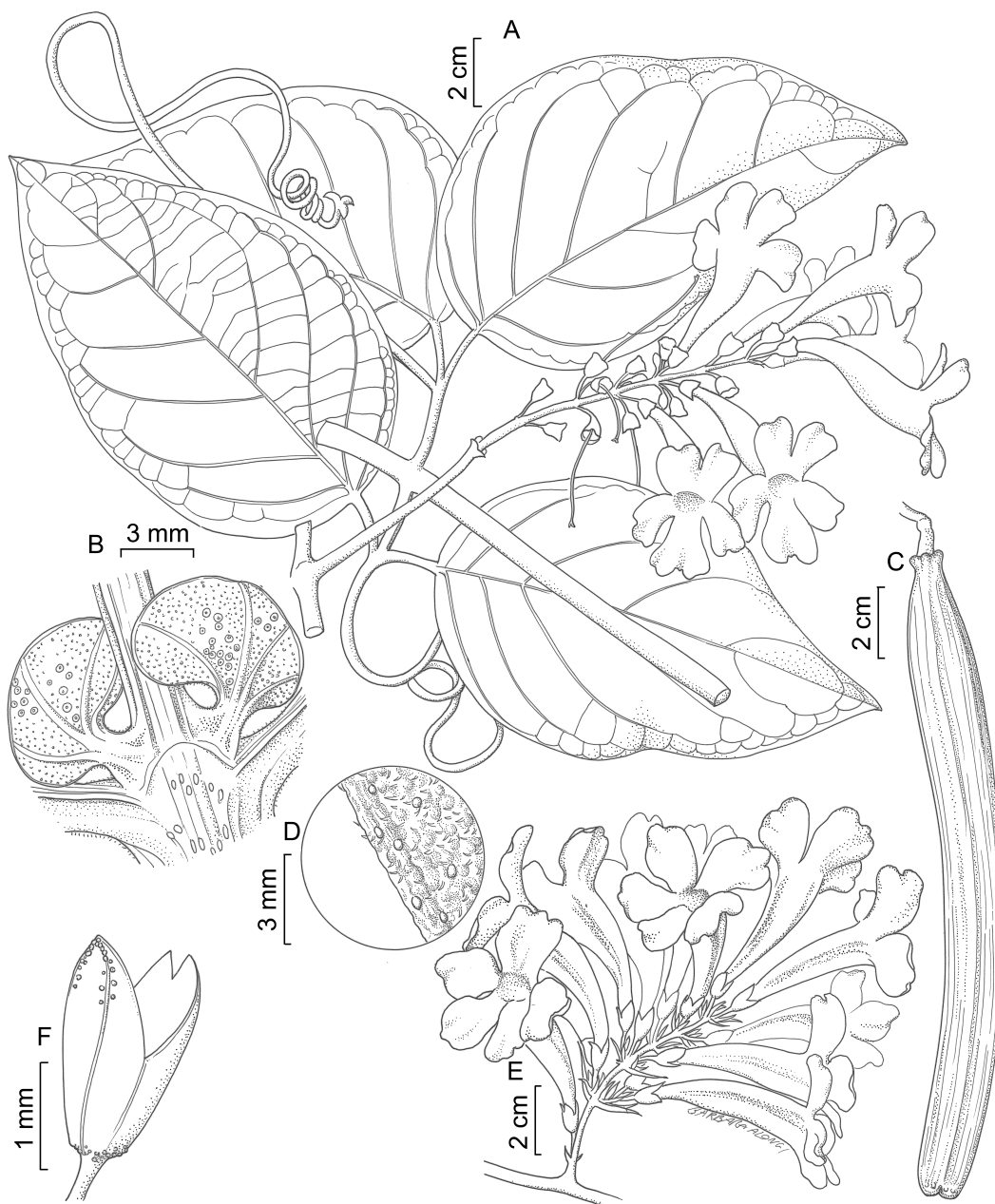


Figure 27 Morphology of *B. bracteomana* (K. Schum. ex Sprague) L.G. Lohmann and *B. sordida* (Bureau & K. Schum.) L.G. Lohmann. **A–E** *B. sordida*: **A** Habit **B** Detail of node and prophylls **C** Flower in side view **D** Fruit **E** Fruit surface (verrucose); **F–G** *B. bracteomana*: **F** Inflorescence “unit” **G** Calyx in side view. Illustrated from *Mori 17263* (MO) [**AC**], *Santos 85* (MO) [**B**], *Hoffman 5270* (MO) [**DE**] and *Brandbyge 30067* (MO) [**FG**].

Satariapo, -13.866667, -68.2, 300 m, 1 Jun 1990, *Gentry 70842* (MO). COLOMBIA.

Caqueta: Florencia, 41 km. N of Florencia. Disturbed forest margin along road, 1.617, -75.617, 1060 m, 12 Jan 1974, *Gentry 9169* (MO). **Putumayo:** Concepcion, Selva higrofila del Rio Putumayo en las \ margenes del afluente izquierda La

Concepcion, 0.083, -75.36, 225 m, 27 Nov 1940, *Cuatrecasas 10834* (COL, F).

ECUADOR. **Napo**: Nuevo Rocafuerte, Nor-Oriente, Nuevo Rocafuerte, colecciones en riveras del Rio Yasuni Y laguna de Jatuncocha, bosque pluvial tropical, -0.95, -75.416, 200–230 m, 28 Feb 1981, *Jaramillo 4433* (AAU, MO, QCA). **Pastaza**: Rio Bobonaza, Rio Bobonaza. Quilloallpa, below Montalvo. River bank Vegetation, partly above high water level, -2.166, -76.883, 300 m, 17 Jul 1980, *Ollgard 34586* (AAU, MO). **Sucumbios**: Tarapoa, Parroquia Tarapoa. Pozo petrolero Mariann 3. Bosque húmedo Tropical. Bosque primario, ligeramente alterado, suelo plano, transición a bosque inundado. Transectos, -0.133, -76.366, 240 m, 23 Apr 1990, *Cerón 9469* (MO). **Zamora-Chinchi**: Shaimi, Shaimi. Frente a destacamento Militar. Márgen derecha del Río Nangaritza. Bosque primario, -4.3, -78.716, 930 m, 27 Oct 1991, *Palacios 8717* (MO).

PERU. **Amazonas**: Condorcanqui, Rio Cenepa, vicinity of Huampami. ca. 5 km east of Chavez Valdivia. Al lado de chacra de Pedro. En bosque primero, -4.5, -78.5, 200–250 m, 14 Aug 1978, *Kujikat 357* (MO). **Cusco**: Dist. Echarate, Kiteni, Agua Dulce. Bosque seco intervenido, -15.6425, -73.06861, 800 m, 17 Nov 2005, *Huamantupa 7233* (MO). **Huanuco**: Codo del Pozuzo, Codo de Pozuzo: Alluvial fan floodplain of Rio Pozuzo after it emerges from mountains, trail E of settlement, -9.865, -75.494, 450 m, 22 Oct 1982, *Foster 9388* (MO). **Loreto**: Maynas, Rio Tigre-Rio Corrientes, Couvenio IIAP-Petroperu, cocha Shebonal, Caserio Cuchara (Rio Corrientes). Bosque ribereño (no inundable), -3.75, -75.25, 150–170 m, 24 Mar 1987, *Grández 938* (MO). **Madre de Dios**: Parque Nacional Manu, Manu National Park. Cocha Cashu, -12.084, -71.7, 23 Aug 1982, *Emmons 49* (MO). Tambopata, Tambopata Nature Reserve; junction of Rio La Torre and Rio Tambopata, Swamp Trail. Tree Plot, -13.134, -69.567, 250 m, 24 May 1987, *Gentry 57542* (MO). **Pasco**: Dist. Palcazú, carretera Buenos Aires - Villa América. Bosque en borde de Carretera, -10.1725, -75.23138, 350 m, 11 Feb 2006, *Vásquez 30935* (MO, SPF). **Puno**: Rio Tavera, Rio Tavera, ridge top across from mouth of first major tributary, -13.35, -69.666, 500 m, 20 May 1992, *Gentry 76904* (F, MO). **San Martin**: Puerto Pizana, Prov. Mariscal Caceres. Dtto. Tocache Nuevo. Puerto Pizana (margen derecha del Rio Huallaga.), -8.011, -76.659, 2 Jan 1971, *Schunke-Vigo 4608* (F, MO, NY). Tocache Nuevo, Prov. Mariscal Caceres. Dtto. Tocache Nuevo. Environs of Tocache Nuevo. Remnants of woods of Don Roberto Aguilar, -8.184, -76.512, 450 m, 1 Jul 1978, *Plowman 7503* (F, MO). **Ucayali**: Coronel Portillo, Vicinity of LSU base camp, Quebrada Shesha (tributary of Río Abajao), Ca. 65 km NE of Pucallpa, -8.033,

-73.916, 250 m, 25 Jun 1987, *Gentry 58505* (MO).

26. *Bignonia sordida* (Bureau & K. Schum.) L. G. Lohmann in Hokche, Berry & Huber, *Nuevo Cat. Fl. Vasc. Venezuela* 272. 2008 = *Arrabidaea sordida* Bureau & K. Schum., *Fl. Bras.* 8(2): 30. 1896 = *Roentgenia sordida* (Bureau & K. Schum.)

Sprague & Sandwith, *Bull. Misc. Inform. Kew* 1932: 91. 1932.

TYPE: British Guiana [Guyana]. Upper Rupununi River., s. d., *Rich. H. Schomburgk 1296* (holotype: B†, possible duplicates at BM, BR, C, CGE, F, G, K, OXF, P, UPS, US, W).

Fig. 27: A–E

Arrabidaea pullei Sprague, *Bull. Herb. Boissier ser. II*, 6: 373. 1906.

TYPE: Suriname. Saramacca. Jan *A.A. Pulle 170* (lectotype, designated here: U (L), isotype: K)

Description: Lianas. **Stems** solid, cylindrical to tetragonal, not winged, with lenticels (without lenticels), without interpetiolar gland fields, with interpetiolar ridge, minutely villous, moderately lepidote (densely lepidote); prophylls caducous, foliaceous, widely falcate, ascending, stipitate, strongly asymmetrical, 5.0 – 7.9 mm × 3.7 – 6.7 mm, without simple trichomes, densely lepidote, with many glands on abaxial surface; bromeliad-like prophylls absent. **Leaves** 2-foliolate; petiole cylindrical or semi-cylindrical (caniculate), (9.9 –) 18.0 – 28.4 (– 45.0) mm, minutely villous, densely lepidote; petiolules circular (tetragonal), 6.2 – 17.1 mm, minutely villous, densely lepidote; blades concolor, chartaceous (membranous), matte, symmetrical, ovate or elliptic (widely ovate), acute, acuminate or rounded apically, rounded basely, (8.7 –) 13.0 – 21.5 (– 29.0) cm × (3.7 –) 7.2– 9.5 (– 15.1) cm, adaxial surface puberulous to minutely villous at veins and base, sparsely lepidote to lepidote, with few glands dispersed (no glands), abaxial surface without simple trichomes (puberulous over main vein), sparsely lepidote to lepidote, with few glands dispersed (no glands), pocket domatia with trichomes on axils of central vein; venation pinnate, tertiary venations opposite percurrent; tendrils rarely present, simple, without simple trichomes, not lepidote or sparsely lepidote, with apex briefly 2–3-fid. **Inflorescences** thyrse, with lateral dichasia simple and sessile lateral simple dichasia, terminal and lateral, minutely pilose, densely lepidote, primary axis 35.8 – 75.0 mm long; bracts

caducous, linear (widely ovate), $0.3 - 8.2 \times 0.2 - 0.6$ mm, without simple trichomes, densely lepidote, without glands; pedicels $2.9 - 7.7$ mm, without simple trichomes, densely lepidote, without glands. **Flowers** with calyx cupular, truncate (5-apiculate), plane smooth (ribbed), sub-chartaceous, $4.2 - 5.7 \times 3.4 - 5.4$ mm wide at the apex, without simple trichomes, moderately to densely lepidote, with many glands, apicules when present ca. 0.6 mm; corolla white outside, purple inside, infundibuliform, dorso-ventrally flattened, membranous, $32.3 - 72.3$ mm, tube $23.7 - 50.9 \times 1.9 - 3.4$ mm wide at base and $8.2 - 18.0$ mm wide at apex, externally without simple trichomes, moderately to densely lepidote, without glands, internally glabrescent, densely lepidote on lobes, with glandular stipitate trichomes in the base, lobes sub-circular (oblong), $8.8 - 19.7 \times 4.4 - 17.7$ mm; androecium didynamous, with stamens included, the largest $9.9 - 19.0$ mm, the shortest $7.9 - 11.3$ mm, without simple trichomes, not lepidote, with stipitate glandular trichomes at base and insertion, thecae $2.3 - 4.2$ mm, staminode $1.2 - 2.3$ mm; gynoecium $22.5 - 35.2$ mm long, ovary cylindrical, smooth, without simple trichomes, densely lepidote, ovules in 2 series per locule, style sparsely lepidote at base; nectariferous disk reduced. **Fruits** flattened, linear to narrowly oblong, $20.0 - 27.2$ cm long \times $19.0 - 40.0$ mm wide, valves woody, without ridges, smooth, puberulent, sparsely lepidote, without glands. **Seeds** brown, slim, transversally elliptic, symmetrical, $22.0 - 27.3 \times 56.8 - 69.2$ mm, seed body central, lenticular, $0.6 - 0.8$ mm thick, wings 2, opaque with hyaline margin.

Distribution: *Bignonia sordida* is commonly found in the wet forests in the Guyana Shield: **Brazil** (Amapá and Amazonas), **French Guiana** (Cayenne), Guyana (Essequibo), **Surinam** (Sipaliwini and Wanica) and **Venezuela** (Bolívar, Delta Amacuro and Mérida) but there are few collections in Amazonia: **Brazil** (Acre, Amazonas, Pará and Maranhão) and **Peru** (Loreto), distributed from sea level to 610 m (Fig. 26).

Phenology: Flowering specimens were documented throughout the year whereas few fruiting specimens are known, only in February and March.

Discussion: *Bignonia sordida* can be distinguished by the minutely villous racemes with lateral and sessile dichasia, trifid tendrils, widely falcate prophylls and leaf

domatia. This species is quite similar to *B. bracteomana*, but can be distinguished, by the indument (*B. bracteomana* is usually glabrous) and small and caducous bracts in *B. sordida* (large bracts and persistent and in *B. bracteomana*).

The holotype of *Arrabidaea sordida* (Schomburgk 1296) was deposited in B and was probably destroyed. We were no able to find a duplicate, however additional collections remain to be studied. If no duplicate can be found, a neotype will be designated.

In the protologue of the single synonym, *Arrabidaea pullei* Sprague, the author designated the type as been deposited at U (as “Herb. Rheno-Traject.”), but since two collections made by Pulle are cited, 170 and 495, a lectotypification is necessary. Gentry (Gentry 1982a: 329) cited the collection 170 as lectotype and then listed the duplicates at U and K. Since he didn’t clearly state which was the actual lectotype and which was the duplicate (isolectotype in current terms), his attempt of lectotypification is not valid. Here, following both the protologue and Gentry’s observation, we designate as lectotype the specimen Pulle 170 at U, now housed at L (Thiers 2014).

Selected specimens: BRAZIL. **Amapá:** Oiapoque, Mpio. de Oiapoque, BR156, 109 km SSE of Oiapoque on road between Oiapoque and Calcoene. Non-inundated moist forest, 3, -51.5, 6 Dec 1984, *Mori 17251* (F, MG, MO, NY). **Amazonas:** São Paulo de Olivença, basin of creek Belem, -3.567, -68.917, 26 Oct 1936, *Krukoff 8623* (BM, F, MO, NY, U). **Maranhão:** Guajá, Moncao, P.I. Guaja, Rio Turiacu, terra firme forest, -3.116, -46.083, 29 Jun 1987, *Balée 3517* (MEXU, MO, NY). **Pará:** Marabá, Reserva Florestal Rio Doce S.A. a 48 Km de Maraba. Castanhal Piranheira. Mata de terra firme, estrada para colocacao Cacimba, -7.71, -57.81, 13 Nov 1991, *Santos 85* (MO). FRENCH GUIANA. **Cayenne:** Tampoc, Sur le Tampoc: en amont du saut. Koumakou Soula, 3.333333, -53.833333, 25 Mar 1977, *Cremers 4502* (MO). GUYANA. **Essequibo:** Mazaruni River, Upper Mazaruni River Basin. Akapai, mixed evergreen forest, 5.883, -60.616, 470 m, 14 Oct 1960, *Tillett 45685* (MO, NY). SURINAM. **Para:** Jodensavanne, Jodensavanne-Mapanekreek, Surinam R, 5.416667, -54.983333, 3 Nov 1953, *Lindeman 5008* (NY, U). SURINAME. **Brokopondo:** Brownsberg Park, vicinity of Boy Scout complex near main park headquarters, 4.9481944, -55.1828334, 478 m, 8 Feb 2011, *Croat 101985* (MO, SPF); Small islands within 2 km of Tonka Island, NW Brokopondo Stuwmeer Lake, E of

Brownsberg Nature Reserve. Upland forest patches on laterite soil, 4.58333, -55.11666, 15 m, 24 Feb 1998, *Hoffman 5270* (MO). **Sipaliwini**: Godwatra village, 1 km S of Kjana village on Gran Rio, 3.58333, -55.66666, 40 m, 12 Feb 1998, *Hoffman 5249* (MO). VENEZUELA. **Amazonas**: Cerro de la Neblina, Rio Mawarinuma, below Cerro Neblina base camp. Low forested area with many river channels, 0.833, -66.183, 140 m, 16 Apr 1984, *Gentry 46679* (MO). **Bolívar**: Rio Paragua, Rio Paragua, hasta 12 vueltas arriba de la boca del Rio Tonoro, 6.05, -63.783, 175 m, 13 May 1987, *Stergios 10320* (MO, NY). **Delta Amacuro**: Rio Grande, East Of Rio Grande, directly east of El Palmar, swampy maure forest, 8.371, -61.593, 6 Jul 1975, *Gentry 14938* (MO). **Merida**: El Palmar, Territorio Federal Delta Amacuro, Bosque Pluvial, Este de Rio Grande, Este-Noreste de El Palmar, cerca de los limites del Estado Bolivar, Venezuela, 8.038, -61.906, 26 May 1964, *Marcano-Berti 199* (MO, NY).

II. *Bignonia* L. subg. *Bignonia*

Bignonia sect. conjugatae DC., Prod. 9: 146. 1945, nom. superfl. illeg.

TYPE: *Bignonia capreolata* L.

Anisostichus Bureau, Monogr. Bignon. 43. 1864, nom. superfl. illeg.

TYPE: *Anisostichus capreolata* (L.) Bureau [≡ *Bignonia capreolata* L.]

Description: Lianas. **Stems** cylindrical (), not winged, with interpetiolar ridge; prophylls persistent, falcate to elliptic (ovate), ascending, stipitate; bromeliad-like prophylls present. **Leaves** (1–)2-foliolate; blades matte, without leaf domatia; venation pinnate, tertiary venations alternate percurrent; tendrils persistent, multifid, apex with disc. **Inflorescences** undeveloped racemes, axillary. **Flowers** with calyx cupular, 2(–5)-lobed (truncate), plane, smooth, membranous to sub-chartaceous, without glands; corolla yellow or red outside and inside, infundibuliform (widely infundibuliform), without glands; androecium didynamous, with stamens included; gynoecium with ovary cylindrical, smooth, densely lepidote, ovules in 2 series per locule; nectariferous disk developed, annular. **Fruits** flattened, linear, smooth, sparsely lepidote, without glands. **Seeds** slender, symmetrical, seed body central,

flattened, wings 2, translucent.

This subgenus, established here, presents only one species: *B. capreolata*, characterized by lanceolate and basely cordate leaflets, and multifid tendril with apex modified into a disk. This species is the only non-Neotropical species of Bignoniaceae and is restricted to USA.



Figure 28. Distribution of *Bignonia subgenus Bignonia. B. capreolata* L.

27. *Bignonia capreolata* L., Sp. Pl. 2: 624. 1753 = *Doxantha capreolata* (L.) Miers, Proc. Roy. Hort. Soc. London 3: 190. 1863 = *Anisostichus capreolata* (L.) Bureau, Monogr. Bignon. 43, t. 6., 1864.

TYPE: Herb. Clifford: 317, *Bignonia* no. 2 excluding open flower (lectotype,

designated by Reveal 1993, pg. 24: BM [BM000646171] image!)

Fig. 19: A–F, 29

Bignonia capreolata var. *atro-sanguinea* Hook. f., Bot. Mag. 106: tab. 6501. 1880.

TYPE: tab. 6501, Hook. f., Bot. Mag. 106, 1880 (lectotype, designated here, Fig. 29).

Bignonia capreolata f. *lutea* Heineke. Sida 9(3): 263. 1982.

TYPE: USA, Tennessee, Gibson Co.: alluvial ridge in southern bank of the Middle fork of the Forked Deer River, 0.9 mi SE of the jct of Tennessee Hwy 152 and the river, 13 Apr. 1981, *T. Heineke* 2273 (holotype: SIU; isotype: Memphis District Corps of Engineers Herbarium).

Description: Lianas. **Stems** finely hollow, cylindrical (), not winged, with lenticels, without interpetiolar gland fields, with interpetiolar ridge, pubescent (glabrescent) at nodes, sparsely lepidote; prophylls persistent, foliaceous, falcate to elliptic (ovate), ascending, stipitate, asymmetrical (symmetrical), $4.7 - 32.7 \times 2.5 - 21.5$ mm, pubescent to pilose at base, sparsely lepidote, without glands (few glands at abaxial surface); bromeliad-like prophylls present. **Leaves** (1–)2-foliolate; petiole semi-cylindrical, $7.2 - 18.7$ mm, pilose above, very sparsely to sparsely lepidote; petiolules cylindrical or caniculate, $6.8 - 14.4 (- 25.4)$ mm, pilose above, sparsely lepidote (very sparsely lepidote); blades discolor, chartaceous, matte, slightly asymmetrical (symmetrical), lanceolate (narrow elliptic to elliptic), acuminate (caudate) apically, cordate (asymmetrical) basely, $6.2 - 15.1 \times 2.5 - 5.5$ cm, adaxial surface minutely pubescent to minutely pilose over midvein and secondary veins, very sparsely lepidote, without glands (few scattered glands), abaxial surface without simple trichomes, sparsely lepidote, with few scattered glands, without domatia; venation pinnate, tertiary venations alternate percurrent; tendrils always present, multifid, without simple trichomes, not lepidote (sparsely lepidote), with simple or discoid apex. **Inflorescences** reduced racemes, pauciflorae, umbelliform, axillary, without simple trichomes, sparsely lepidote, primary axis $1.0 - 2.2$ mm long; bracts persistent (caducous), triangular, $1.4 - 2.8 \times 0.6 - 1.2$ mm, without simple trichomes, very sparsely lepidote, without glands; pedicels $11.0 - 31.8$ mm, without simple trichomes, sparsely lepidote, without glands. **Flowers** with calyx cupular, 2(–5)-lobed (truncate), plane, smooth, membranous (sub-chartaceous), $5.4 - 11.0 \times 5.3 - 12.2$ mm wide at

apex, ciliate, sparsely lepidote, without glands, lobes 1.6 – 4.2 mm; corolla red outside, red or yellow inside, infundibuliform (widely-infundibuliform), not flattened, membranous to sub-chartaceous, 41.3 – 61.7 mm, externally with pubescent tube and pilose lobes (entirely pubescent), very sparsely lepidote (only dorsally sparsely lepidote), without glands, internally pilose at stamens insertion and pubescent at lobes, not lepidote, without glandular trichomes, tube 33.9 – 49.3 × 2.6 – 5.6 mm wide at base and 10.9 – 20.4 mm wide at apex, lobes triangular or oblong (widely oblong), 7.8 – 16.7 × 6.9 – 12.1 mm; androecium didynamous, with stamens included (exserted), the largest 21.6 – 28.8 mm, the shortest 16.3 – 24.7 mm, pilose (pubescent) at base (entirely glabrescent), not lepidote, without glandular trichomes, thecae 3.2 – 4.6 mm, staminode 5.2 – 8.0 mm; gynoecium 32.0 – 44.5 mm, ovary cylindrical, smooth, without simple trichomes, densely lepidote, ovules in 2 series, style not lepidote; nectariferous disk developed, 1.3 – 2.3 × 2.5 – 3.3 mm. **Fruits** flattened, linear, 11.6 – 16.1 × 15.8 – 16.5 wide × 3.8 – 4 cm thick, valves woody, without ridges, smooth, without simple trichomes, sparsely lepidote, without glands. **Seeds** beige, slim, narrowly depressed ovate, symmetrical, 9.5 – 10.7 × 35.5 – 36.3 mm, seed body central, flattened, 0.9 – 1.0 mm thick, wings 2, partially translucent.

Distribution: *B. capreolata* is the single non-Neotropical species of Bignoniaceae. It is found mostly along rivers and is restricted to USA (Alabama, Arkansas, Florida, Georgia, Illinois, Kentucky, Louisiana, Maryland, Mississippi, Missouri, North Carolina, South Carolina, Tennessee, Texas, Virginia, West Virginia), from sea level to 1100 m. It is also widely cultivated *** (MAP_CAPREOLATA).

Phenology: Flowers are documented from February to September, but are more common in April and May. Fruiting specimens were collected from February to October.

Discussion: This species is characterized by the always-present multifid tendrils, lanceolate and basally cordate leaflets, and pauciflorae inflorescences with red or yellow flowers. The prophylls of *B. capreolata* are also distinctive because only in this species the shape changes throughout its development: the prophylls are initially subulate and subsequently a flat surface begins to develop until reaching the final form (falcate or elliptic), becoming progressively larger in older nodes. *Bignonia*



Figure 29. Lectotype of *B. capreolata* var. *atro-sanguinea* Hook. f. From Bot. Mag. 106: tab. 6501. 1880. Image obtained from Biodiversity Heritage Library.

capreolata is the only species of Bignoniaceae native to USA, so it can be distinguished

from local Bignoniaceae just by the presence of tendrils (absent in all non-Bignoniaceae lianas). The multifid tendrils may also help to distinguish *B. capreolata* from other Bignoniaceae that are cultivated or spontaneous in US in which tendrils are simple or trifid (except for *Amphilophium crucigerum* (L.) L.G. Lohmann, where the stems are hexagonal and ribbed).

Two infra-specific taxa have been described for *B. capreolata*, one distinguished only by yellow flowers (*B. capreolata* f. *lutea*) and the other (*B. capreolata* var. *atro-sanguinea*) by longer and red flowers. These characters are too variable, sometimes even in the same specimen, creating a gradient between these morphotypes, as recognized by Hooker in the protologue of the later taxa. In this protologue, no type is formally indicated however an illustration is provided based on a cultivated specimen at Kew. To avoid future misinterpretations of vouchers from this specimens made after the publication of this variety, we here designate the illustration as lectotype, since it matches the description and captures the diagnostic features indicated by Hooker.

Selected specimens: UNITED STATES. **Alabama:** Mobile, Streambank; 0.5 miles east of the Mississippi state line on U.S. route 90, 30.47983999999999, -88.40012, 14 Mar 1976, *Boufford 2832* (MO). **Arkansas:** Pulaski, North facing bluff. Pulaski Heights. Little Rock, 34.746388, -92.289444, 10 Aug 1931, *Demaree 8480* (MO). **Florida:** Bordering Telogia Creek at route 12 bridge, NE edge of Greensboro, 30.56859, -84.72070999999999, 7 Jul 1977, *Loran 4495* (MO). **Georgia:** De Kalb/, at edge of outcrop, Mt. Arabia, 33.66499999999999, -84.118333, 24 Apr 1957, *Burbank 1542* (MO). **Illinois:** Alexander, Low woods, Cairo, Illinois, 37.005277, -89.176388, 23 Apr 1919, *Palmer 14926* (MO). **Kentucky:** Cliffs of Kentucky River. High Bridge, Ky, 37.817222, -84.71999999999999, 13 May 1923, *Frank 18* (MO). **Louisiana:** Bienville/, Low wooded bottom along Black Lake Creek and Illinois Central Gulf R.R. at junction of parish road and U.S. 80, 33, -93, 20 Mar 1974, *William 173* (MO). **Maryland:** Somerset, Vicinity of Pocomoke City; along River Road just before it meets Dividing Creek Rd, 300 yds from U.S. 13; along edge of road, 38.14115999999999, -75.50894999999999, 2 m, 14 May 1987, *Bunting 13516* (MO). **Mississippi:** Hancock, 3.4 miles east of the Pearl River County Line on Miss. route 48, woods over and along a small creek, 30.52053, -89.53024, 3 Jun 1976, *Boufford 18667* (MO). **Missouri:** Stoddard, T25N, R10E, sec 1, 2 miles NE of Dexter,

Missouri. Low woods bordering spring branch, 36.81533, -89.92343999999999, 17 May 1984, *Summer 1380* (MO). **North Carolina**: Madison, 1.5 mi. W of Hot Springs. Railroad right-of-way along south bank of French Broad River, 35.89934, -82.86139, 8 May 1976, *Solomon 1472* (MO). **South Carolina**: Abbeville, ca 10 km S of Abbeville: Sumter National Forest, 34.11710999999999, -82.37045999999999, 23 Jul 1989, *Thompson 6665* (MO). **Tennessee**: Cheatham, Thickets along rocky stream, near Kingston Springs, Tenn, 36.101944, -87.11499999999999, 24 Apr 1929, *Palmer 35513* (MO). **Texas**: Angelina, 11 miles south of Nacogdoches, floodplain of Angelina River, 31.5148, -94.72659, 29 Mar 1972, *John 9873* (UMO). **Virginia**: Accomack, 8 Jun 1958, *Reed 41444* (MO). **West Virginia**: Wayne, Roadside, climbing over trees. Near Crum, 37.905555, -82.446111, 16 Apr 1938, *Williams 689* (MO).

III. *Bignonia* subg. *Osmhydrophora* (Barb. Rodr.) Zuntini, stat. et comb. nov. = *Osmhydrophora* Barb. Rodr., *Vellosia*, ed. 2, 1: 49. 1891, *Osmhydrophora*, orth. var. TYPE: *Bignonia nocturna* (Barb. Rodr.) L. G. Lohmann

Description: Lianas. **Stems** cylindrical, not winged, without interpetiolar ridge; prophylls minute; bromeliad-like prophylls absent. **Leaves** 2-foliolate; blades matte, without leaf domatia; venation actinodromous, tertiary venations alternate percurrent; tendrils persistent, simple, with simple apex. **Inflorescences** thyrsi, terminal, lateral or axillary. **Flowers** with calyx tubular, truncate or 5-apiculate, plane, smooth, membranous to sub-coriaceous, with glands; corolla white outside and inside, narrowly infundibuliform, with glands; androecium dydimous, with stamens exerted; gynoecium with ovary tetragonal, smooth, densely lepidote, ovules in 4 series per locule; nectariferous disk developed, annular. **Fruits** 4-lobed or (cylindrical), narrowly oblong (narrowly elliptic), smooth, moderately lepidote (sparsely lepidote), with scattered glands. **Seeds** slender, asymmetrical, seed body central, flattened, wings 2, translucent (opaque).

Bignonia subg. *Osmhydrophora* is recognizable by the leaflets with actinodromous venation, white and tubular corolla with gland fields and a cylindrical fruits. Another unique character found in this subgenus is the curved staminode,

which is straight is all other species.

A single species, *B. nocturna*, distributed throughout Amazonia up to Southern Panama (Fig. 30).



Figure 28. Distribution of *Bignonia subgenus Osmhydrophora*. *B. nocturna* (Barb. Rodr.) L.G. Lohmann.

28. *Bignonia nocturna* (Barb. Rodr.) L. G. Lohmann, Nuevo Cat. Fl. Vasc.

Venezuela 272. 2008 = *Osmhydrophora nocturna* Barb. Rodr., Vellozia, ed. 2, 1: 49,

3: tab. 8, 9. 1885–1888 [1891] = *Tanaecium nocturnum* (Barb. Rodr.) Bureau & K.

Schum., Fl. Bras. 8(2): 185. 1896.

Type: Vellozia 3, ser. 2: tab. 8, pg. 50. 1891 (lectotype, designated here, Fig. 31).

Figs. 31, 32

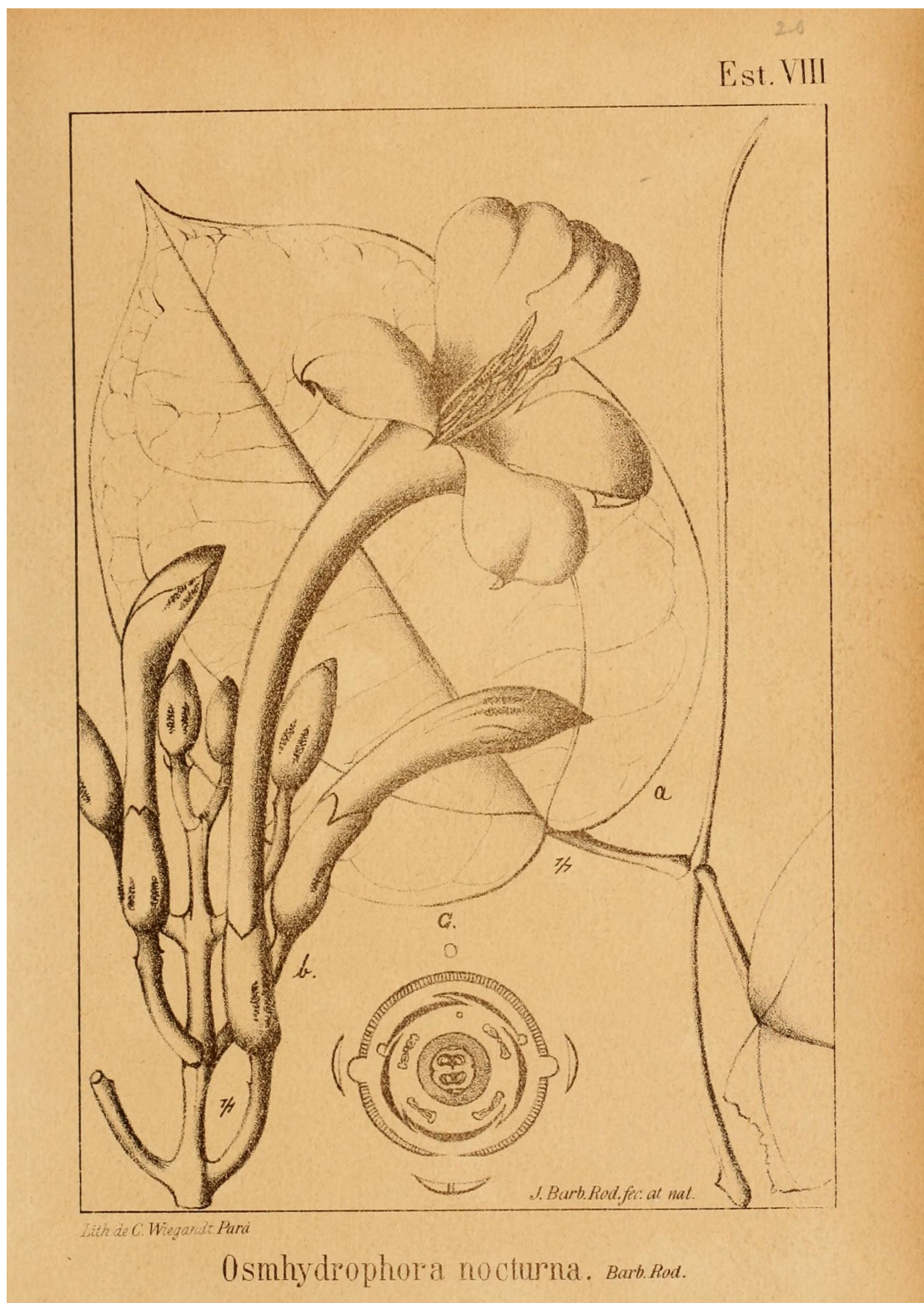


Figure 31. Lectotype of *B. nocturna* (Barb. Rodr.) L.G. Lohmann. From *Vellosia*, ed. 2, 1: 49, 3: tab. 8 1885–1888 [1891]. Image obtained from Biodiversity Heritage Library.

Description: Lianas. **Stems** solid, cylindrical, not winged, without lenticels (with lenticels), without interpetiolar gland fields, without interpetiolar ridge, without simple trichomes, (glabrescent), sparsely lepidote; prophylls minute; bromeliad-like prophylls absent. **Leaves** 2-foliolate; petiole cylindrical, 39.4 – 67.8 (– 87.0) mm, without simple trichomes, very sparsely to sparsely lepidote; petiolules cylindrical, 18.8 – 76.0 mm, without simple trichomes, very sparsely to sparsely lepidote; blades concolor, chartaceous (sub-chartaceous), matte, symmetrical, widely elliptic to circular (elliptic), acuminate apically, rounded to truncate basely, 6.8 – 19.0 (–21.5) × 4.0 – 14.6 (–18.5) cm, adaxial surface without simple trichomes, very sparsely lepidote (sparsely lepidote), without glands, abaxial surface without simple trichomes, very sparsely lepidote (sparsely lepidote), with many glands at base and few dispersed (no or just few scattered glands), without domatia; venation actinodromous, tertiary venations alternate percurrent; tendrils always present, simple, without simple trichomes, sparsely lepidote, with simple apex. **Inflorescences** thyrsi, with lateral dichasia simple (compound) and pedunculate, pauciflorae, racemiform, terminal, without simple trichomes, sparsely lepidote (moderately to densely lepidote), primary axis 49.0 – 195.0 mm long; bracts caducous, linear, 2.0 – 4.3 × 0.3 – 0.5 mm, without simple trichomes, moderately lepidote, without glands; pedicels 3.1 – 9.9 mm, without simple trichomes, moderately to densely lepidote, without glands. **Flowers** with calyx tubular, truncate (5-apiculate), plane, smooth, sub-coriaceous, 14.7 – 20.5 × 6.9 – 8.4 mm wide at the apex, without simple trichomes (ciliate), moderately lepidote, with many glands organized in 5 longitudinal lines, apicules when present ca. 0.7 mm; corolla white, yellow or greenish outside, white inside, narrowly infundibuliform, not flattened, chartaceous, 66.6 – 137.6 mm, externally without simple trichomes, not lepidote (very sparsely lepidote), with many glands in 5 clustered below lobes, internally pilose near calyx height, not lepidote, with glandular sessile trichomes in the lobes, tube 56.5 – 93.6 × 3.3 – 7.8 mm wide at base and 8.7 – 20.0 mm wide at apex, lobes oblong, 12.0 – 38.2 × 6.2 – 20.2 mm; androecium dydimous, with stamens exserted, 25.6 – 49.8 mm, without simple trichomes, not lepidote, without glandular trichomes, thecae 5.4 – 8.6 mm, staminode 0.8 – 1.6 mm; gynoecium (67.0 –) 86.2 – 97.3 mm, ovary tetragonal, smooth, without simple trichomes, densely lepidote, ovules in 4 series per locule, style not lepidote; nectariferous disk developed, 2.6 – 3.9 mm × 1.6 – 2.0 mm, glabrous. **Fruits** 4-lobed (cylindrical), narrowly oblong (narrowly elliptic), 12.1 – 19.8 × 2.3 – 5.1 wide × 3.3 –

4.2 cm thick, valves petrous, without ridges, smooth, without simple trichomes, moderately lepidote (sparsely lepidote), with few scattered glands. **Seeds** brown, slim, narrowly transversally elliptical, asymmetrical, 11.0 – 21.0 × 31.9 – 76.5 mm, seed body central, flattened, 1.6 – 2.1 mm thick, wings 2, translucent (opaque).

Distribution: *Bignonia nocturna* is found in evergreen forest in **Bolivia** (Beni, La Paz, Pando, Santa Cruz), **Brazil** (Acre, Amazonas, Goiás, Mato Grosso, Pará, Rondônia), **Colombia** (Antioquia, Bolivar, Chocó, Córdoba, Santander), **French Guiana** (Cayenne, Mariposula, Saint-Laurent-du-Maroni, Saül), **Panama** (Darién), **Peru** (Amazonas, Cusco, Huánuco, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), **Surinam** (Nickerie, Sipaliwini) and **Venezuela** (Amazonas), from sea level to 700 m (Fig. 30).

Phenology: Flowering and fruiting collections are recorded throughout the year, with flowers more abundant between November and January.

Discussion: This species is very distinctive by the almond smell in the stem and leaves, actinodromous venation, white, long and narrowly infundibuliform corolla, with many glands in clusters at lobes' bases, dydimous androecium and cylindrical fruits. This combination of characters is unique not only in *Bignonia*, but in the whole tribe, which led to the description in its own genus (*Osmhydrophora*).

The flower morphology and the nocturnal anthesis are characteristic of phalaenophilous flowers, a pollination syndrome rarely found in Bignoniaceae. All species of Bignoniaceae with this flower morphology were gathered in *Tanaecium* Sw. (Bureau et al. 1896, Gentry 1974a), including *B. nocturna*, despite its morphological divergence from remaining species, such as actinodromous venation and phloem wedges in multiple of 4 vs. pinnate venation and 4 wedges in the phloem (Lohmann and Taylor 2014).

The type collection of *Osmhydrophora nocturna*, gathered near Manaus, in the forests by the River Purus, was supposedly deposited at INPA or RB, but almost all Barbosa Rodrigues' types were destroyed (Mori and Ferreira 1987). Moreover, on a recent survey no specimen that predates the species description was found in either of these herbaria, making the two plates cited in the protologue the only remaining original materials. The first plate (Tab. 8, here designated as lectotype) contains all

diagnostic characters of *O. nocturna* [\equiv *B. nocturna*] such as markedly actinodromous venation, long tubular corolla, linear gland clusters at calyx and below lobes of the corolla, exserted stamens and the four series of ovules per locule. The second plate provides additional details of reproductive characters, like opened corolla (inside and outside), lateral views of calyx, ovary and the prominent nectariferous disk, and cross-sections of the ovary, depicting the placentation.

The almond smell is result of the essential oils found in this species, majorly benzaldehyde (Fazolin et al. 2007). These oils are present in high concentrations, and due to their hallucinogenic properties, *B. nocturna* has been widely used by native populations in South America (reviewed in Gentry 1992a).

Selected specimens: BOLIVIA. **Beni:** Puerto de Florida, Puerto de Florida, Río Beni, -11, -66, 13 Sep 1985, *Moraes 581* (MO). **La Paz:** Alto Beni, Alto Beni, -15.533333, -67.35, 600 m, 28 Dec 1987, *Schulte 1005* (MO). **Pando:** Conquista, 18 km hacia el Puerto sobre el Río Madre de Dios-via Sena, -11.4, -67.183333, 8 Oct 1991, *Beck 20231* (MO). **Santa Cruz:** Parque Nacional Noel Kempff Mercado. 15 km de los Fierros camino saliendo por El Encanto. Bosque alto con: *Coriniana estrillensis*, *Pseudolmedia*, *Brosimum*, *Vochysia* y *Erismia*. *Sustraro duricosta* Ferruginoso y latosol, -14.635278, -60.781389, 200 m, 11 Apr 1994, *Guillén 1262* (MO, USZ).

BRAZIL. **Acre:** Rio Branco, 20 km from Río Branco on Río Branco-Porto Acre road, -10, -67.815, 11 Oct 1980, *Lowrie 476* (MO, NY). **Amapá:** s.loc., 1.5159364, -51.8554687, 15 Sep 1960, *Irwin 48260* (NY). **Amazonas:** s.loc., 17 Dec 1945, *Ducke 1843* (F, NY). **Goiás:** Rio Piranhas, Rio Piranha, Ihla S. Izabel, afl. do Araguaia, -5.933, -48.25, 16 May 1961, *Oliveira 1710* (IAN, MO). **Mato Grosso:** Matupá, Rodovia BR 80, Faz. Cachimbo. Mata, terra firme, solo argiloso, -10.0575, -54.93278, 18 Nov 1976, *Cordeiro 1059* (MO, NY). **Pará:** Rio Jari, Regiao Rio Jari, Pilao, Igarape do Bandeira, -1.15, -51.9, 23 Jan 1969, *Silva 1673* (COL, MO, NY).

Rondônia: Basin of Rio Madeira. Trail from Fortaleza, Rio Abunã 20 km above mouth to São Sebastiao Mines, -9.7, -65.53, 15 Nov 1968, *Prance 8482* (F, NY).

COLOMBIA. **Amazonas:** Puerto Nariño, Km 6 de la trocha de Puerto Nariño a la Quebrada Amacayacu, -3.77, -70.383, *Diaz 9* (NY). **Antioquia:** San Luis, Municipio de San Luis, Cañon del Rio Claro, 5.883, -74.65, 4 Jun 1984, *Cogollo 1814* (MO). **Bolívar:** Barranca Bermeja, 150 km N of Barrancabermeja \ Mico-Ahumado camp, 8.25, -74.066, 18 Aug 1966, *Bruijn 1046* (COL, MER, MO, VEN). **Choco:** Parque

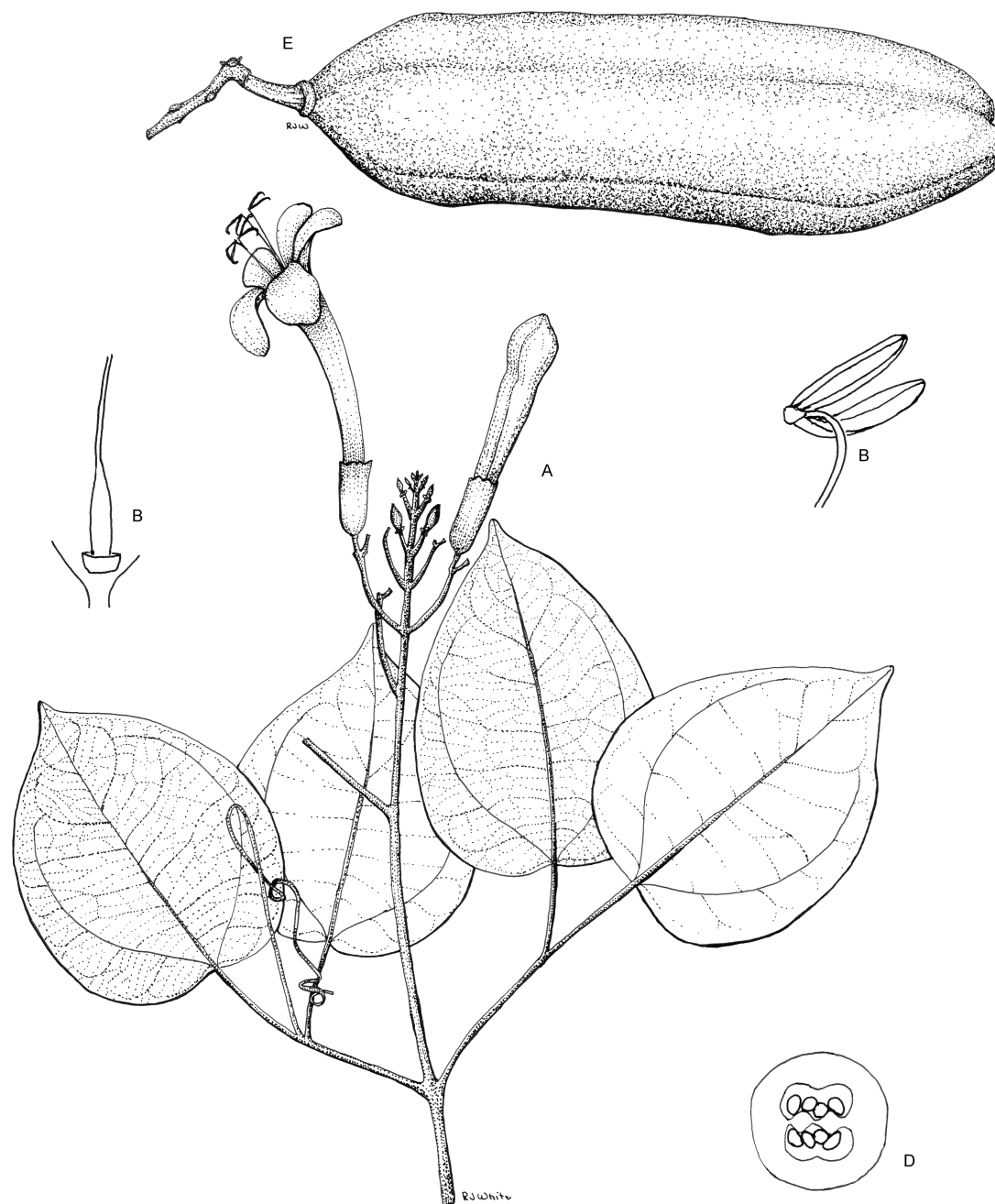


Figure 32. Morphology of *B. nocturna* (Barb. Rodr.) L.G. Lohmann. **A** Habit **B** Fruit **C** Ovary with developed disk **D** Anther **E** Ovary cross-section. Illustrated from *Tyson 4808, Britan 1061 and Gentry 4543* (MO) [**A**], *Gentry 6926* (MO) [**B**] and *Gentry 5233* (MO) [**C–E**]. From Gentry (1973: 956, fig. 37).

Nat. Los Katios \ Alrededores de Campamento de Tilupo, 7.817, -77.18, 250–260 m, 30 May 1976, *Forero 1693* (COL, MO). **Cordoba**: Palotal, Palotal, 8.86, -75.896, 4 Jul 1948, *Romero-Castaneda 1135* (MO). **Santander**: Campo Capote, Las Colonias, Carare-Opon, 6.618, -73.914, 240 m, 11 Jun 1979, *Renteria 1556* (MO, NY).

FRENCH GUIANA. **Cayenne**: Saul, Bourg Saul - Reigon de Saul, 3.616, -53.216, 200 m, 12 May 1986, *Sauvain 641* (CAY, MO). PANAMA. **Darien**: Rio Tuquesa, Between Quebrada Venado and Peje Swamp, Rio Tuquesa, 8.383, -77.783, 28 Jun 1967, *Bristan 1061* (MO, SCZ). PERU. **Amazonas**: Imaza, Distrito Imaza: Región del Marañon. Comunidad de Yamayakat, Río Marañon. Bosque primario, -4.91666, -78.31666, 550 m, 20 Jan 1995, *Vásquez 19331* (F, MO). **Cusco**: Pilcopata, Pilcopta, Atalaya, Paucartambo, -13.066, -71.166, 650 m, 15 Jan 1987, *Nunez 6886* (F, MO). **Huánuco**: Rio Cuchara, Santa Tiofila (Rio Cuchara), -9.02, -76.117, 19–20 m, 9 Nov 1961, *Schunke-Vigo 5731* (F, MO). **Loreto**: Rio Pucayacu, Pucayacu, (Comunidad Nativa Shimaco-Urarina) Bosque primario, -3.666, -77.416, 7 Dec 1984, *Vásquez 6025* (MO, NY). **Madre de Dios**: Tambopata, Tambopata Tourist Camp. Trail to Coca Cocha Lake, -13.134, -69.567, 260 m, 17 Dec 1992, *Gentry 78181* (MO). **Pasco**: Oxapampa, Vivero of Proy. Pichis Palcazu, Rio Pichis below and across from Puerto Bermudez. Lowland, tropical moist forest, probably formely much disturbed, -10.2, -74.95, 200 m, 16 Jun 1983, *Gentry 42102* (MO). **San Martin**: Mariscal Caceres, Prov. Mariscal Caceres. En bosque alto, -7.833, -76.666, 500–700 m, 12 Nov 1975, *Schunke-Vigo 8671* (MO). **Ucayali**: Pucallpa, In tall forest at Pucallpa, -8.382, -74.538, 200 m, 1 Dec 1965, *Schunke-Vigo 982* (F, MO, NY). SURINAME. **Bajkutu**: s.loc., 25 Feb 1985, *Sauvain 292* (MO). **Benakofondre**: s.loc., 24 Jun 1984, *Sauvain 163* (MO). **Nickerie**: Avanavero, Rain forest, ca 3 km S of road camp, where old road crosses the new one, ca 22 km SW of Avanavero dam site, 4.833333, -55.016667, 17 Nov 1976, *Heyde 129* (MO). **Sipaliwini**: Kjana village, Vicinity of Kjana village on Gran Rio, 3.58333, -55.66666, 40 m, 14 Jul 1998, *Plotkin 1357* (MO).

VENEZUELA. **Amazonas**: Río Mavaca. Selvas h'medas siempre-verdes de planicies bajas con sectores de rebalse estacional y de arroyos; y de planicie de tierra firme hasta pié de lomerio, 7 Feb 1991, *Stergios 15255* (MO, NY).

IV. *Bignonia* subg. *Saritaea* (Dugand) Zuntini, stat. et comb. nov. = *Saritaea* Dugand, *Caldasia* 3: 262. 1945.

TYPE: *Bignonia magnifica* W. Bull

Pyrostegia sect. *Macranthisiphon* Baill. *Hist. Pl.* 10: 31. 1891 [1888] =

Macranthisiphon (Baill.) Bureau ex K. Schum., *Nat. Pflanzenfam.* 4(3b): 219. 1894.

TYPE: *Bignonia longiflora* Cav.

Description: Lianas (shrubs). **Stems** cylindrical, not winged, with or without interpetiolar ridge; prophylls persistent, elliptic, ascending, stipitate; bromeliad-like prophylls absent (present). **Leaves** 1–2-foliolate; blades matte or laevigate, without leaf domatia; venation actinodromous or pinnate, tertiary venations alternate percurrent; tendrils persistent, simple, with simple apex. **Inflorescences** compound dichasia or thyrsi, terminal (axillary). **Flowers** with calyx tubular, truncate or shortly 5-lobed, plane or 5-costate, smooth, chartaceous, with or without glands; corolla orange or pink outside and inside, infundibuliform or narrowly infundibuliform, without glands; androecium didynamous, with stamens included or exerted; gynoecium with ovary cylindrical, smooth, densely lepidote, ovules in 2 series per locule; nectariferous disk developed, annular. **Fruits** flattened, linear, smooth, moderately lepidote, with scattered glands. **Seeds** slender, symmetrical, seed body central, flattened, wings 2, translucent.

This subgenus is characterized by the stipitate and elliptic prophylls, polyporate pollen with complex exine patterns and fruits with scattered glands. Laevigate leaflets are also commonly observed, although not always present. The affinity of the two species has been previously hypothesized based on the unique pollen morphology (Gentry et al. 1979) but the contrasting flower morphologies, tubular and orange in *B. longiflora* vs. infundibuliform and pink or magenta in *B. magnifica*, led to the maintenance of each species in its own monotypic genus, *Macranthisiphon* and *Saritaea*.

The two included species are restricted to Colombia, coastal Ecuador and Venezuela; *B. magnifica* is widely cultivated (Fig. 33).

29. *Bignonia longiflora* Cav., Icon. 6: 58, tab. 581. 1801, non Willd. in DC., Prodr. 9: 206. 1845, nom. nud. pro syn., nec Vell., Fl. Flumin.: 252. 1829 = *Pyrostegia longiflora* (Cav.) Miers, Proc. Roy. Hort. Soc. London 3: 188. 1863 = *Macranthisiphon longiflorus* (Cav.) K. Schum., Nat. Pflanzenfam. 4(3b): 219. 1894. TYPE: Ecuador. Guayaquil, s. d., L. Nee s.n. (lectotype, designated by Lohmann & Taylor (2013: 421): MA-652465!, MA-652465 as photo F neg. 29231 at MO-1692897!; isolectotypes: B †, as photo F neg at MO-1692898!; MA-475442 image!;

possible isoelectotype: F-842390!)

Fig. 34

Bignonia guayaquilensis DC., Prodr. 9: 155. 1845.

TYPE: Ecuador. Guayaquil, August 1836, C. Gaudichaud 93 (lectotype, designated here: P [P00608091] image!; isoelectotypes: K [K000449545] image!, LP-2872 image!, P [P00608092, P00608093] image!, S-04-3492 image!, US [US002515304] image!).

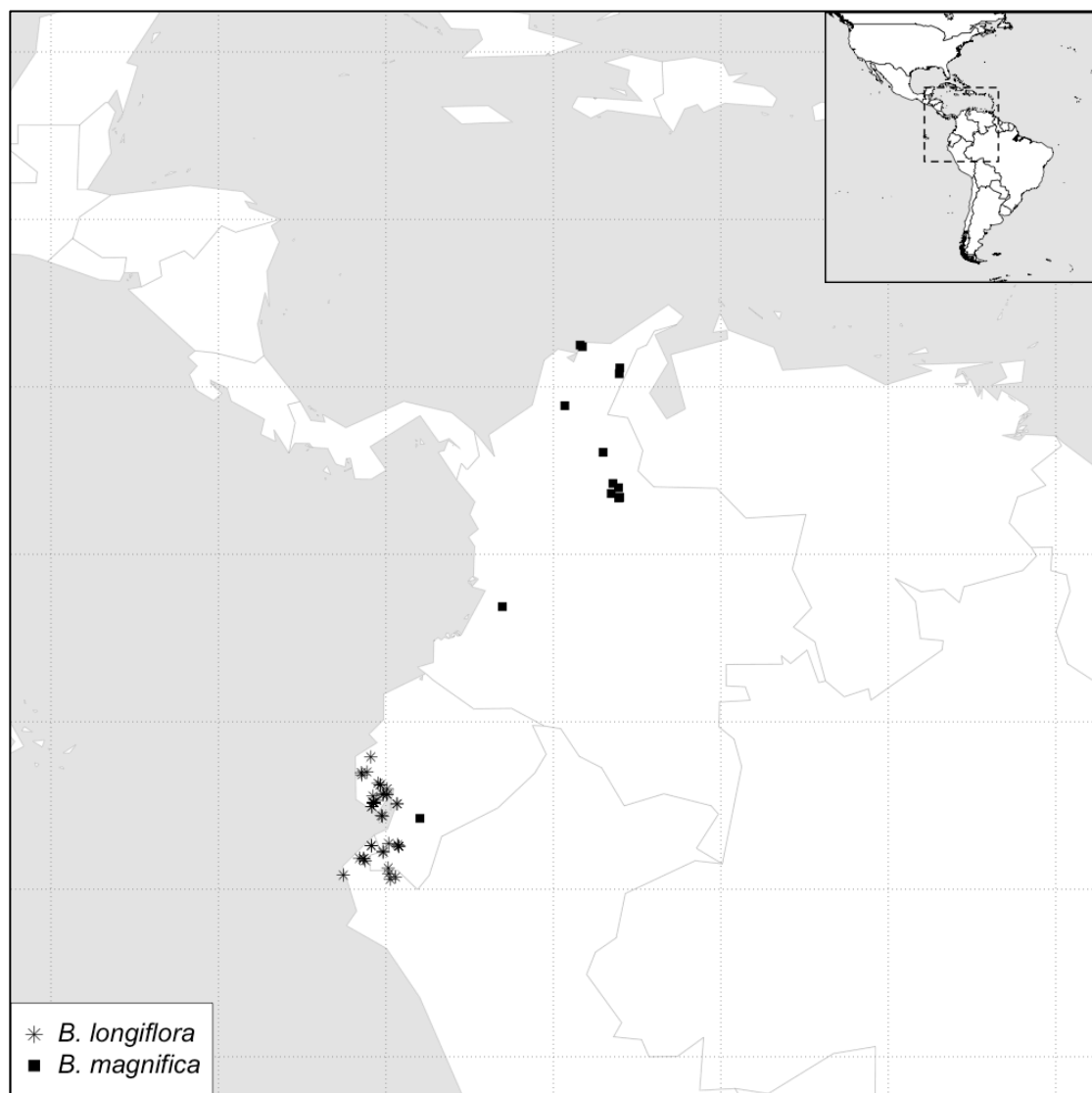


Figure 33. Distribution of *Bignonia* subg. *Saritaea*. *B. longiflora* Cav. (asterisk), and *B. magnifica* W. Bull (solid square)

Description: Lianas (shrub). **Stems** solid, cylindrical, not winged, with (without) lenticels, without interpetiolar gland fields, without interpetiolar ridge, without simple trichomes, moderately lepidote; prophylls persistent, foliaceous, elliptic or oval (circular), ascending, stipitate, symmetrical, 6.4 – 23.3 mm × 3.3 – 14.2 mm, without simple trichomes, moderately lepidote, with glands near the base on abaxial surface (glands absent), bromeliad-like prophylls absent. **Leaves** 1–2-foliolate; petiole caniculate or semicircular, 4.6 – 16.6 (–62.0) mm, without simple trichomes, moderately lepidote; petiolules caniculate (semicircular), 2.1 – 7.6 (– 13.7) mm, without simple trichomes, not lepidote; blades discolor (concolor), chartaceous (sub-chartaceous), matte abaxially and laevigate adaxially (completely matte), symmetrical, narrowly elliptic, acuminate apically, rounded or cuneate basely, (11.2 –) 36.0 – 115.3 × (3.6 –) 11.0– 42.0 cm, adaxial surface without simple trichomes, moderately lepidote (sparsely lepidote), without glands, abaxial surface without simple trichomes, moderately lepidote, with few to many glands near the base and occasionally sparse in the blade (no glands), without domatia; venation sub-actinodromous, tertiary venations alternate percurrent; tendrils usually present, simple, without simple trichomes, not lepidote, with simple apex. **Inflorescences** thyrse, with lateral dichasia simple and pedunculate (solitary flowers), pauciflorae, racemiform, terminal (axillary), without simple trichomes, moderately lepidote, primary axis (2.8 –) 13.5 – 69.4 (– 156.0) mm long; bracts caducous, narrowly triangular, 1.2 – 1.7 × 0.3 – 0.8 mm, without simple trichomes, moderately lepidote, without glands; pedicels 10.1 – 27.6 mm, without simple trichomes, moderately lepidote, without glands. **Flowers** with calyx tubular, truncate (shortly 5-lobed), 5-costate, smooth, chartaceous, 4.5 – 7.3 × 3.9 – 5.9 mm wide at the apex, without simple trichomes, moderately lepidote (sparsely lepidote), with many scattered glands, lobes when present 0.3 – 1.2 mm long; corolla orange (reddish) outside and inside, narrowly infundibuliform, not flattened, sub-chartaceous, 62.9 – 102.4 mm, externally without simple trichomes, moderately lepidote (moderately lepidote only at lobes), without glands, internally with lobes pubescent, moderately lepidote at lobes, without glandular trichomes, tube 48.1 – 77.3 × 2.6 – 4.1 wide at base and 10.1 – 17.4 mm wide at apex, lobes rectangular or obovate, 10.0 – 22.7 × 5.0 – 12.0 mm; androecium didynamous, with stamens exserted, the largest (32.7 –) 46.6 – 68.9 mm, the shortest (28.4 –) 45.5 – 62.3 mm, without simple trichomes, not lepidote, without glandular trichomes, thecae 4.3 – 5.8 mm, staminode 2.6 – 9.3 mm; gynoecium 55.0 –

94.9 mm, ovary cylindrical, smooth, without simple trichomes, densely lepidote, ovules in 2 series per locule, style not lepidote (minutely lepidote); nectariferous disk developed, 1.2 – 1.9 × 2.2 – 2.9 mm. **Fruits** flattened, linear, 15.5 – 20.4 × 0.9 – 1.5 wide × 0.1 – 0.3 cm thick, valves woody, without ridges, smooth, glabrescent, moderately to densely lepidote, with many scattered glands. **Seeds** brown, slim, rectangular, symmetrical, 9.1 – 11.8 × 29.0 – 36.0 mm, seed body central, flattened, 0.3 – 0.9 mm thick, wings 2, translucent.

Distribution: This species is distributed in western **Ecuador** (El Oro, Guayas, Loja and Manabí) and northern **Peru** (Piura and Tumbes). It occurs in seasonal vegetation, from sea level to 800m (Fig. 33).

Phenology: Flowers during wet season (June to October) and fruits almost the same period (July to October). By the end of this season is common finding collections with both flowers and fruits.

Discussion: When bearing flowers, this species is rapidly distinguishable narrowly infundibuliform, orange corolla. Also, the foliaceous, elliptic and persistent prophylls can also help identifying this species. These characters can also be found in *B. magnifica*, but this differs from *B. longiflora* by primary venation [actinodromous vs. pinnate] and the leaflet base [attenuate vs. rounded to cuneate].

Bignonia longiflora is one of the few species in tribe Bignonieae that is pollinated by hummingbirds and due to morphological convergence to this syndrome it was once placed in genus *Pyrostegia*. This species is clearly not a member of this genus due to the cylindrical and not ribbed stem (vs. hexagonal and ribbed), simple tendril (vs. trifold) and foliaceous prophylls (minute in *Pyrostegia*). Actually, *B. longiflora* is closely related to *B. magnifica* (Zuntini & Lohmann, in prep.), a species probably pollinated by bees; both species share pollen with complex ornamentation (Gentry et al. 1979) and elliptic, glandular prophylls.

The Cavanille's type collections are deposited in Madrid (MA), including the lectotype of *B. longiflora*. However, one of specimens identified as “*Cavallinesii* typi” (MA-475431) doesn't seem to be a duplicate of type collecting and shouldn't be treated an isolectotype. The morphology is too different from the other specimens and the handwriting appears to be from someone else than Cavanille's.



Figure 34. Morphology of *B. longiflora* Cav. **A** Flowering branch **B** Stem cross-section **C** Fruits. Illustrated from *Gentry 12238* (MO) [**A–B**] and *Gentry 10000* (MO) [**C**]. From Gentry (1977)

When de Candolle published *B. guayaquilensis*, he only stated that the type was in P. Three sheets are deposited in this herbarium, one of which tagged as type, while the other two as isotypes; however no formal designation was ever published. Hence, here we formally designate the first specimen (P00608091), containing both

flowers and fruits, as lectotype.

The name *Bignonia longiflora* was used to describe two other species: the first, that would predate Cavanille's publication, was attributed to Karl Willdenow, by De Candolle (1945), as a possible synonym for *Spathodea rheedii* Spreng.

[=*Dolichandrone spathacea* (L.f.) Seem.]. This name wasn't validly published so it doesn't qualify as a true homonym. The other use of *B. longiflora* was made by Vellozo (1929) to describe a tree species from Brazil; this posterior homonym was later noticed and corrected by Toledo (1952), with the proposition of a new name: *Tabebuia vellosi* Toledo [= *Handroanthus vellosi* (Toledo) Mattos].

Selected specimens: ECUADOR. **El Oro:** Portovelo, Portovelo, -3.716667, -79.616667, 600–1000 m, 30 Aug 1923, *Hitchcock 21236* (MO, NY). **Guayas:** Guayaquil, 19 km S of Jipijapa on road to Guayaquil, -2.416, -80.366, 300 m, 29 Oct 1974, *Gentry 12211* (MO). **Loja:** Macara, Checkpoint 1 km E Macara on road to Sozoranga, -4.366, -79.933, 450 m, 29 Jan 1991, *Kessler 2292* (GOET, MO). **Manabí:** Portoviejo, 11 km SW of Portoviejo: 13 km N of Montichristi, -1.05, -80.45, 300 m, 7 Aug 1980, *Hansen 7978* (MO, tampa). PERU. **Piura:** Ayabaca, Sullana, Palo Blanco, Sullana-Ayabaca, -4.633, -79.716, 450 m, 25 May 1971, *Lopez 7682* (MO, NY, TRUJ). **Tumbes:** El Caucho, Zarumilla, region below El Caucho, -4.074, -80.786, 350–450 m, 18 Feb 1976, *Plowman 5502* (MO).

30. *Bignonia magnifica* W. Bull in W. Richards, Gard. Chron., n. s. 12(290): 72, fig. 9. 1879; also Retail List New Beautiful Rare Pl. 154: 4, 1879, *nom. cons. prop.* = *Arrabidaea magnifica* (W. Bull) Sprague ex Steenis, Receuil Trav. Bot. Néerl. 24: 830. 1927 = *Sarिताea magnifica* (W. Bull) Dugand, Caldasia 3: 263. 1945.

TYPE: Colombia. Magdalena: Santa Marta, 1500 ft., Sep. 1898–1901, H.H. Smith 741, *typ. cons. prop.* (type: L [L0003408] image!; isotypes: BM!, BR [BR0000008579850] image!, K [K000404058, K000404059] image!, MO-2005575!, NY [NY00313101, NY00313102] image!, S04-3464, UC-584951 image!, US-600311 image!).

Fig. 35

Description: Lianas. **Stems** solid, cylindrical, not winged, with lenticels, without interpetiolar gland fields, with or without interpetiolar ridge, without simple

trichomes, moderately lepidote (not lepidote); prophylls persistent, foliaceous, elliptic to circular, ascending, stipitate, symmetrical, 10.0 – 38.6 mm × 4.4 – 24.1 mm, without simple trichomes, moderately lepidote, with many glands near the base on abaxial surface, bromeliad-like prophylls absent (present). **Leaves** 1–2-foliolate; petiole semicircular (caniculate), 12.1 – 35.9 mm, without simple trichomes, moderately lepidote (not lepidote); petiolules caniculate, 2.8 – 8.5 (– 11.5) mm, without simple trichomes, moderately lepidote (not lepidote); blades discolor, sub-chartaceous to chartaceous, laevigate (matte), symmetrical, obovate (elliptic), briefly-acuminate (rounded) apically, attenuate basely, 5.8 – 12.1 × 2.6 – 5.9 cm, adaxial surface without simple trichomes, moderately lepidote (not lepidote), without glands, abaxial surface without simple trichomes, moderately lepidote, with many glands near the base, without domatia; venation actinodromous, tertiary venations alternate percurrent; tendrils usually present, simple, without simple trichomes, moderately lepidote (not lepidote), with simple apex. **Inflorescences** compound dichasia, multiflorae, corymbiform, terminal, primary axis (7.5 –) 28.1 – 69.4 mm long, lepidote; bracts caducous, narrowly triangular (spathulate), 1.2 – 4.0 (– 8.1) mm × 0.3 – 1.0 (– 2.3) mm, without simple trichomes, moderately lepidote (not lepidote), without glands; pedicels 10.6 – 22.9 (– 29.1) mm long, without simple trichomes, moderately lepidote (not lepidote), without glands. **Flowers** with calyx tubular, truncate, plane, smooth, chartaceous, 9.4 – 11.4 × 6.0 – 7.2 mm wide at the apex, without simple trichomes, moderately lepidote (not lepidote), without glands (few scattered glands); corolla pink to magenta outside and inside, infundibuliform, not flattened, membranous, (55.1 –) 70.5 – 94.7 mm, externally without simple trichomes, moderately lepidote (not lepidote), without glands, internally without simple trichomes, moderately lepidote at lobes, without glandular trichomes, tube 41.0 – 66.3 × 3.0 – 5.1 mm wide at base and 11.4 – 27.4 mm wide at apex, lobes rounded, (13.9 –) 19.7 – 28.2 mm × (14.1 –) 21.9 – 35.5 mm; androecium didynamous, with stamens included, the largest 18.5 – 32.0 mm, the shortest 14.1 – 21.5 mm, without simple trichomes (pilose at the base), not lepidote, without glandular trichomes, thecae 3.2 – 6.3 mm, staminode 4.9 – 6.5 mm; gynoecium (32.6 –) 41.9 – 53.7 mm, ovary cylindrical, smooth, without simple trichomes, densely lepidote, ovules in 2 series per locule, style not lepidote (sparsely lepidote); nectariferous disk developed, 0.9 – 1.8 mm × 1.8 – 3.1 mm, glabrous (lepidote). **Fruits** flattened, linear, 15.7 – 28.2 × 0.7 – 1.1 cm wide × ca. 0.1 cm thick, valves woody, without ridges, smooth, without simple

trichomes, moderately lepidote, with few scattered glands. **Seeds** beige or brown, slim, rectangular, symmetrical, $23.1 - 32.7 \times 7.6 - 11.8$ mm, seed body central, flattened, 0.6 – 0.8 mm thick, wings 2, translucent.

Distribution: This species is naturally distributed in wet forests of **Colombia** (Cesar, Guajira, Magdalena, Santander and Valle del Cauca) and is commonly cultivated worldwide (Fig. 33).

Phenology: Flowering collections are most common between June and December and fruiting collections between July and November.

Discussion: Besides by the showy flowers, *B. magnifica* can be easily recognized by the obovate leaflets, with attenuate base and the big gland field near the base, making this portion of the leaflet slightly translucent. These gland are often located on other parts, like branches, leaflets blade and floral buds, where a viscid secretion is produced, leaving the surfaces irregularly shiny. This same process appears to happen in the corolla lobes of *B. longiflora*, denoting another shared features between these species.

Regarding the distribution of *B. magnifica*, it is quite difficult to delineate its natural distribution since this species has been used as ornamental since its description. Here, we chose a more strict approach, considering it restricted to Northern Colombia.

The taxonomic history of *B. magnifica* is controversial. This species was described by William Bull with a brief description and an illustration. Since no material is cited, the illustration is the only known original material and therefore would automatically be the holotype (McNeill et al. 2012: Art. 9.1). Later, van Stennis provided a full description of *Arrabidaea magnifica*, accrediting this species to Sprague and designated a type. However, in a footnote, he mentioned that this name was a combination of *B. magnifica* W. Bull, intended to be made by Sprague. In this case, the designation of the type made by van Stennis is invalid since the holotype is extant. Unfortunately, the species described by Stennis, which represents the current concept of *B. magnifica*, is not the same as that from W. Bull, as later noticed by Sprague himself, on a letter sent to van Steenis. However, since the combination was effective, the name *A. magnifica* is bonded to the original description, making the

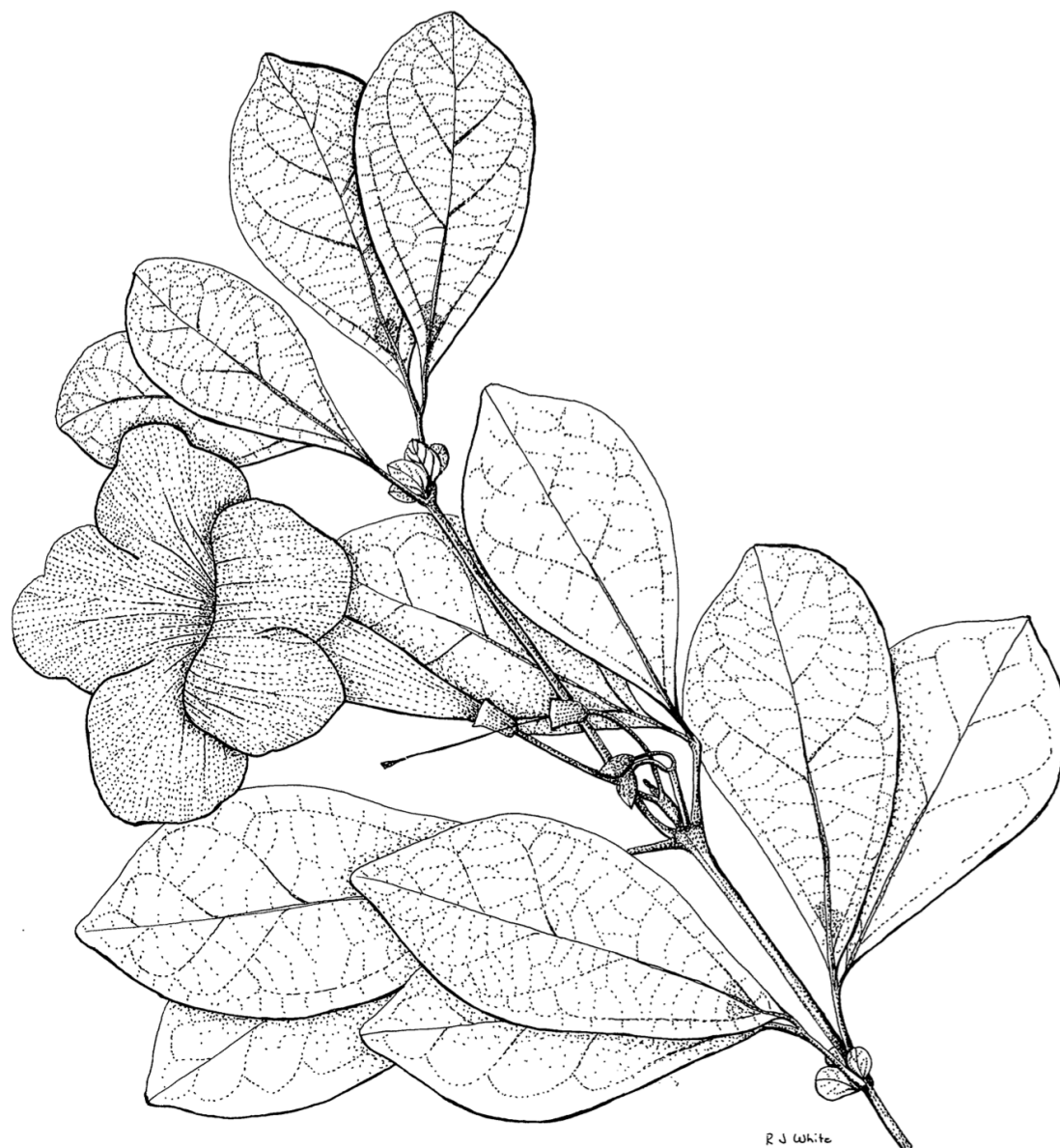


Figure 35. Morphology of *B. magnifica* W. Bull. Flowering branch. Illustrated from Gentry 6049 (MO). From Gentry (1973: 921, fig. 31).

currently usage of *B. magnifica* meaningless. To correct this mistake and maintain the taxonomic stability, the conservation of the type designated by van Steenis was proposed (Zuntini, Taylor & Lohmann, in prep.; Cap. 1)

Selected specimens: COLOMBIA. **Cesar:** Manaure Balcon del Cesar, La Paz a Manaure, 10.392, -73.032, 80 m, 26 Apr 1987, *Cuadros 3446* (F, JBG, MO).

Guajira: Urumita, Urumita, just S of Villanueva, 10.566, -73.016, 17 Sep 1938, *Haught 2342* (COL, MO, NY). **Magdalena:** Santa Marta, Santa Marta, 11.247, -

74.201, 500 m, Sep 1898-1901, *Smith 741* (Isótipo, MO). **Santander:** Aratoca, 3 km

N of Aratoca, disturbed roadside;, 6.698, -73.021, 1600 m, 23 Jul 1975, *Gentry 15345* (COL, MO). Piedecuesta, Between Piedecuesta & Las Vegas, 6.989, -73.053, 1200–2000 m, 19 Dec 1926, *Killip 15462* (A, GH, NY). **Valle Cauca:** Cali, Cali, 3.437, -76.522, 900 m, 16 Nov 1983, *Forero 1539* (MO). ECUADOR. **Azuay:** Cuenca, Chullabamba, 10 km north of Cuenca in the Cuenca Valley near the river. Plants collected on the country estate of Marcelo Jaramillo, -2.883611, -78.983611, 2350 m, 8 Oct 1981, *Dodson 11697* (MO).

Nomina dubia

- Bignonia acutiflora* Mart. ex DC., Prodr. 9: 181. 1845
- Bignonia aesculus* Desf., Tabl. École Bot., ed. 3: 397. 1829
- Bignonia affinis* G. Don, Gen. Hist. 4: 217. 1837
- Bignonia angrensis* Vell., Fl. Flumin.: 246. 1825 [1829]
- Bignonia argentea* Sessé & Moc., Fl. Mexic., ed. 2: 146. 1894
- Bignonia aurantiaca* W.Bull, Cat.. 1874
- Bignonia auriculigera* Mart. ex Colla, Herb. Pedem. 4: 182. 1835
- Bignonia bidwilliana* Regel, Cat. Pl. Hort. Aksakov.: 19. 1860
- Bignonia bijuga* Vahl, Symb. Bot. 2: 68. 1791
- Bignonia cymosa* Vell., Fl. Flumin.: 249. 1825 [1829]
- Bignonia doniana* DC., Prodr. 9: 145. 1845
- Bignonia ecirrhata* Larrañaga, Escritos D. A. Larrañaga 2: 189. 1923
- Bignonia fraxinea* Desf., Tabl. École Bot., ed. 3: 398. 1829
- Bignonia gigantea* Noronha, Verh. Batav. Genootsch. Kunsten 5(4): 8. 1790
- Bignonia grandiflora* Sessé & Moc., Fl. Mexic., ed. 2: 146. 1894, hom. illeg.
- Bignonia jasminoides* A.Cunn. ex DC., Prodr. 9: 225. 1845, hom. illeg.
- Bignonia leucoxydon* Sessé & Moc., Fl. Mexic., ed. 2: 145. 1894

- Bignonia macrocalyx* Pedersoli, Oréades 1(2): 13. 1970
- Bignonia macrophylla* Sessé & Moc., Pl. Nov. Hisp.: 99. 1889
- Bignonia maranhamensis* DC., Prodr. 9: 165. 1845
- Bignonia marmorata* André, Rev. Hort.: 253. 1865
- Bignonia meridionalis* Salisb., Prodr. Stirp. Chap. Allerton: 106. 1796
- Bignonia micranthera* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 148. 1874
- Bignonia mina* C.P.Robin, Voy. Int. Louisiane 3: 408. 1807
- Bignonia muricata* Sessé & Moc., Pl. Nov. Hisp.: 99. 1889
- Bignonia nigricans* Regel, Cat. Pl. Hort. Aksakov.: 19. 1860
- Bignonia ornata* E.Morren, Ann. Hort. Belge Etrangère 17: 102. 1867
- Bignonia peltata* B.Otto & A.Dietr., Allg. Gartenzeitung 9: 58. 1841
- Bignonia pentandria* Larrañaga, Escritos D. A. Larrañaga 2: 189. 1923
- Bignonia punioides* Griff., Itin. Pl. Khasyah Mts. 227: 202. 1848
- Bignonia quinquefolia* Sessé & Moc., Fl. Mexic., ed. 2: 145. 1894
- Bignonia regalis* W.Bull, Cat.. 1885
- Bignonia reveilii* Hamon, Bull. Soc. Hortic. Prat. Dép. Rhône: 148. 1851
- Bignonia rhodosantha* Zipp. ex Blume, Rumphia 4: 35. 1836
- Bignonia rodigasiana* L.Lind., Ill. Hort. 11: 89. 1893
- Bignonia sambucifolia* Carrière, Rev. Hort.: 50. 1878
- Bignonia sempervirens* L., Sp. Pl. 2: 623. 1753
- Bignonia splendor-sylvae* Mart. ex DC., Prodr. 9: 154. 1845
- Bignonia ternata* G. Don, Gen. Hist. 4: 221. 1837, hom. illeg.
- Bignonia tinctoria* Arruda, in H.Koster, Trav. Brazil: 497. 1817
- Bignonia triflora* Vell., Fl. Flumin.: 249. 1825 [1829]
- Bignonia violacea* DC., Prodr. 9: 156. 1845

Invalid names, including nomina nuda

- Arrabidaea decora* var. *genuina* Hassl., Repert. Spec. Nov. Regni Veg. 9: 49. 1910.
- Bignonia bellas* Sellow ex Steud., Nomencl. Bot., ed. 2, 1: 204. 1840, nom. nud.
- Bignonia chrysophylla* Klotzsch, in R.Schomburgk, Reis. Br.-Guiana 3: 969. 1848, nom. nud.
- Bignonia crenata* Lodd. ex Loudon, Hort. Brit.: 242. 1830, nom. nud.
- Bignonia decipiens* Lodd. ex Loudon, Hort. Brit.: 242. 1830, nom. nud.
- Bignonia dura* Klotzsch ex R.Knuth, Feddes Repert. Beih. 43: 638. 1827, nom. nud. = *Tabebuia insignis* (Miq.) Sandwith
- Bignonia filicifolia* Anderson, Trans. Soc. London Encour. Arts. 25: 200. 1807, nom. nud. = *Jacaranda obtusifolia* Bonpl.
- Bignonia fraxinoides* Perr., Mém. Soc. Linn. Paris 3: 102. 1824, nom. nud.
- Bignonia gaudichaudii* DC., Prodr. 9: 172. 1845, nom. nud. = *Lundia cordata* (Vell.) DC.
- Bignonia inaequilatera* Poepp. ex Bureau & K. Schum., in . C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 8(2): 222. 1896, nom. nud. ≡ *Stizophyllum inaequilaterum* Bureau & K. Schum.
- Bignonia karstenii* Klotzsch ex Bureau & K. Schum., in . C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 8(2): 130. 1896, nom. nud. ≡ *Anemopaegma karstenii* Bureau & K. Schum.
- Bignonia laciniata* Hunter ex Ridl., J. Straits Branch Roy. Asiat. Soc. 53: 101. 1909, nom. inval. = *Stereospermum fimbriatum* (Wall. ex G. Don) DC.
- Bignonia lucida* Lodd. ex Loudon, Hort. Brit.: 242. 1830, nom. nud.
- Bignonia multifida* Lodd. ex Loudon, Hort. Brit.: 242. 1830, nom. nud.
- Bignonia ophthalmica* Chisholm ex Steud., Nomencl. Bot., ed. 2, 1: 205. 1840, nom. nud.
- Bignonia pachyptera* DC., Prodr. 9: 174. 1845, nom. nud. = *Dolichandra uncata* (Andrews) L.G.Lohmann

Bignonia parviflora Salzm. ex DC., Prodr. 9: 183. 1845, nom. nud. = *Fridericia rego*
(Vell.) L.G.Lohmann

Bignonia petiolaris DC., Prodr. 9: 174. 1845, nom. nud.

Bignonia purpurea Lodd. in DC. Prod. 9: 171. 1845, nom. nud.

Bignonia quadrangularis Lockh. ex Steud., Nomencl. Bot., ed. 2, 1: 205. 1840, nom.
nud.

Bignonia reticulata Poepp. ex Bureau & K. Schum., in . C.F.P. von Martius & auct.
suc. (eds.), Fl. Bras. 8(2): 82. 1896, nom. nud. = *Fridericia poeppigii* (DC.)
L.G.Lohmann

Bignonia robusta Klotzsch, in R.Schomburgk, Reis. Br.-Guiana 3: 969. 1848, nom.
nud. ≡ *Anemopaegma robustum* Bureau & K. Schum.

Bignonia sonderi Bureau ex Corr.Méllo, Arq. Mus. Paranaense 9: 108. 1952, nom.
inval.

Bignonia sordida Klotzsch, in R.Schomburgk, Reis. Br.-Guiana 3: 969. 1848, nom.
nud. ≡ *Bignonia sordida* (Bureau & K. Schum.) L. G. Lohmann

Bignonia spicata Lockh. ex Steud., Nomencl. Bot., ed. 2, 1: 205. 1840, nom. nud.

Bignonia striata DC., Prodr. 9: 174. 1845, nom. nud. = *Tanaecium pyramidatum*
(Rich.) L.G.Lohmann

Bignonia subincana Hemsl., Biol. Cent.-Amer., Bot. 2: 491. 1882, nom. nud. invalid.
Fridericia candicans (Rich.) L.G.Lohmann

Bignonia surinamensis Klotzsch, in R.Schomburgk, Reis. Br.-Guiana 3: 969. 1848,
nom. nud.

Bignonia viridiflora Lodd., Bot. Cab. 11: t. 1026. 1825, nom. nud. = *Cybistax*
antisyphilitica (Mart.) Mart.

Phrygiobureaua corymbosa (Vent.) Kuntze, Ann. Missouri Bot. Gard. 99(3): 348–
489. 2014, nom. nud. pro syn.

Species exclusae

- Anisostichus crucigera* (L.) Small, Man. S.E. Fl.: 1240. 1933 ≡ *Amphilophium crucigerum* (L.) L.G.Lohmann
- Bignonia acapulcensis* Kunth ex Baill., Hist. Pl. 10: 28. 1888 = *Fridericia mollissima* (Kunth) L.G.Lohmann
- Bignonia acuminata* J.R.Johnst., Proc. Amer. Acad. Arts 40: 696. 1905 = *Fridericia dichotoma* (Jacq.) L.G.Lohmann
- Bignonia acutissima* Cham., Linnaea 7: 691. 1832 = *Adenocalymma comosum* (Cham.) DC.
- Bignonia acutistipula* Schltl., Linnaea 26: 375. 1854 = *Dolichandra unguis-cati* (L.) L.G.Lohmann
- Bignonia adenophylla* Wall., Numer. List 6502: 221. 1832 ≡ *Fernandoa adenophylla* (Wall. ex G. Don) Steenis
- Bignonia adenophylla* Wall. ex G. Don, Gen. Hist. 4: 22. 1837 ≡ *Fernandoa adenophylla* (Wall. ex G. Don) Steenis
- Bignonia adhatodifolia* Jacq., Fragm. Bot.: 61. 1800 = *Anemopaegma grandifolium* (Jacq.) Merr. & Sandwith
- Bignonia aequinoctialis* var. *chamberlaynii* (Sims) Ker Gawl., Bot. Reg. 9: t. 741. 1823 = *Anemopaegma chamberlaynii* (Sims) Bureau & K. Schum.
- Bignonia aesculifolia* Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 140. 1818 [1819] ≡ *Godmania aesculifolia* (Kunth) Standl.
- Bignonia africana* Lam., Encycl. 1: 424. 1785 ≡ *Kigelia africana* (Lam.) Benth.
- Bignonia agnus-castus* Cham., Linnaea 7: 673. 1832 = *Fridericia rego* (Vell.) L.G.Lohmann
- Bignonia alata* Pav. ex DC., Prodr. 9: 224. 1845 = *Tecoma fulva* (Cav.) G. Don
- Bignonia alba* Aubl., Hist. Pl. Guiane 2: 653. 1775 = *Adenocalymma album* (Aubl.) L.G.Lohmann
- Bignonia albida* Blume, Catalogus: 81. 1823 = Gesneriaceae
- Bignonia albiflora* Salzm. ex DC., Prodr. 9: 167. 1845 ≡ *Pleonotoma albiflora*

(Salzm. ex DC.) A.H. Gentry

Bignonia alliacea Lam., Encycl. 1: 421. 1785 ≡ *Mansoa alliacea* (Lam.) A.H. Gentry

Bignonia amara Loudon ex G. Don, Gen. Hist. 4: 222. 1937 = *Radermachera gigantea* (Blume) Miq.

Bignonia amoena Wall., Pl. Asiat. Rar. 2: 78. 1831 = *Radermachera gigantea* (Blume) Miq.

Bignonia anastomosans DC., Prodr. 9: 144. 1845 = *Phyllarthron ilicifolium* (Pers.) H. Perrier

Bignonia andrieuxii DC., Prodr. 9: 156. 1845 = *Fridericia floribunda* (Kunth) L.G.Lohmann

Bignonia angustifolia (Blume) Blume, Catalogus: 82. 1823 = Gesneriaceae

Bignonia antisiphilitica Mart., in J.B. von Spix & C.F.P. von Martius, Reise Bras. 1: 283. 1823 ≡ *Cybistax antisiphilitica* (Mart.) Mart.

Bignonia apurensis Kunth, in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. Pl. 3: 138. 1818 [1819] ≡ *Adenocalymma apurense* (Kunth) Sandwith

Bignonia aquatilis E.Mey., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 12: 780. 1825 = *Tabebuia fluviatilis* (Aubl.) DC.

Bignonia araliacea Cham., Linnaea 7: 683. 1832 = *Handroanthus serratifolius* (Vahl) S.O.Grose

Bignonia argyrea André, Rev. Hort.: 251. 1865 = Asteraceae

Bignonia argyreoviolascens Lem., Ill. Hort.: t. 469. 1866 = Asteraceae

Bignonia arrabidaei Steud., Nomencl. Bot., ed. 2, 1: 204. 1840 = *Stizophyllum perforatum* (Cham.) Miers

Bignonia artherion Mart., Flora 24(2) (Beibl. 3): 47. 1841 = *Fridericia artherion* (Mart.) L.G.Lohmann

Bignonia articulata Desf., in J.B.A.P.M. de Lamarck, Encycl., Suppl. 1: 636. 1811 ≡ *Phyllarthron articulatum* (Desf.) K. Schum.

- Bignonia arvensis* Vell., Fl. Flumin.: 250. 1825 [1829] ≡ *Anemopaegma arvense*
(Vell.) Stellfeld ex De Souza
- Bignonia atrovirens* Roth, Nov. Pl. Sp.: 284. 1821 ≡ *Dolichandrone atrovirens*
(Roth) K. Schum.
- Bignonia atrovirens* DC., Prodr. 9: 171. 1845 = *Tabebuia elliptica* (DC.) Sandwith
- Bignonia aurea* Silva Manso, Enum. Subst. Braz.: 40. 1836 ≡ *Tabebuia aurea*
(Silva Manso) Benth. & Hook.f. ex S. Moore
- Bignonia australis* (R. Br.) Aiton, Hortus Kew. 4: 34. 1812 = *Pandorea*
pandorana (Andrews) Steenis
- Bignonia azedarachta* König & Sims, Ann. Bot. 9(König & Sims) 1: 578. 1805 =
Millingtonia hortensis L.f.
- Bignonia baclei* DC., Prodr. 9: 171. 1845 = *Amphilophium cynanchoides* (DC.)
L.G.Lohmann
- Bignonia balbisiana* DC., Prodr. 9: 153. 1845 = *Fridericia dichotoma* (Jacq.)
L.G.Lohmann
- Bignonia balbisiana* var. *glabra* DC., Prodr. 9: 153. 1845 = *Fridericia dichotoma*
(Jacq.) L.G.Lohmann
- Bignonia balbisiana* var. *hirsuta* DC., Prodr. 9: 153. 1845 = *Fridericia dichotoma*
(Jacq.) L.G.Lohmann
- Bignonia banaibanai* (Bureau) Callery ex Burch., Adansonia 2: 195. 1862 =
Radermachera pinnata (Blanco) Seem.
- Bignonia barbata* E.Mey., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 12:
782. 1825 ≡ *Handroanthus barbatus* (E.Mey.) Mattos
- Bignonia benensis* Britton ex Rusby, Bull. Torrey Bot. Club 27: 70. 1900 =
Pachyptera kerere (Aubl.) Sandwith
- Bignonia bibracteata* Bertol. ex DC., Prodr. 9: 240. 1845 = Acanthaceae
- Bignonia bifaria* Lhotsky & Manso ex Bureau & K. Schum., in C.F.P. von
Martius & auct. suc. (eds.), Fl. Bras. 8(2): 125. 1896 = *Anemopaegma*
brevipes S. Moore

- Bignonia bipinnata* Salzm. ex DC., Prodr. 9: 230. 1845 = *Jacaranda obovata* Cham.
- Bignonia blanchetii* DC., Prodr. 9: 164. 1845 = *Fridericia pubescens* (L.) L.G.Lohmann
- Bignonia bojeri* DC., Prodr. 9: 165. 1845 = *Ophiocolea floribunda* (Bojer ex Lindl.) H. Perrier
- Bignonia boliviana* Rusby, Bull. Torrey Bot. Club 27: 70. 1900 = *Fridericia dichotoma* (Jacq.) L.G.Lohmann
- Bignonia botryoides* Cham., Linnaea 7: 100. 1832 = *Amphilophium crucigerum* (L.) L.G.Lohmann
- Bignonia brachiata* Sessé & Moc., Fl. Mexic., ed. 2: 146. 1894 = *Tanaecium pyramidatum* (Rich.) L.G.Lohmann
- Bignonia brachypoda* DC., Prodr. 9: 145. 1845 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia brachypoda* var. *acutifolia* DC., Prodr. 9: 145. 1845 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia brachypoda* var. *cuneata* DC., Prodr. 9: 145. 1845 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia brachypoda* var. *elliptica* DC., Prodr. 9: 145. 1845 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia brachypoda* var. *firmula* DC., Prodr. 9: 146. 1845 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia brachypoda* var. *heterophylla* DC., Prodr. 9: 145. 1845 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia brachypoda* var. *platyphylla* (Cham.) DC., Prodr. 9: 145. 1845 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia brachypoda* var. *pubescens* Sond., Linnaea 22: 559. 1849 = *Fridericia platyphylla* (Cham.) L.G.Lohmann
- Bignonia bracteata* Cham., Linnaea 7: 692. 1832 ≡ *Adenocalymma bracteatum*

(Cham.) DC.

Bignonia bracteolata DC., Prodr. 9: 157. 1845 ≡ *Fridericia bracteolata* (DC.)

L.G.Lohmann

Bignonia bracteosa DC., Prodr. 9: 165. 1845 = *Rhodocolea involucrata* (Bojer ex

DC.) H. Perrier

Bignonia brasiliana Lam., Encycl. 1: 425. 1785 ≡ *Jacaranda brasiliana* (Lam.)

Pers.

Bignonia brevipes Rusby, Bull. Torrey Bot. Club 27: 71. 1900 = *Stizophyllum*

riparium (Kunth) Sandwith

Bignonia buccinatoria (DC.) Mairet ex Hemsl., Biol. Cemt.-Amer., Bot. 2: 490.

1882 ≡ *Amphilophium buccinatorium* (DC.) L.G.Lohmann

Bignonia caerulea L., Sp. Pl. 2: 625. 1753 ≡ *Jacaranda caerulea* (L.) Juss.

Bignonia californica Brandegee, Zoe 5: 170. 1903 = *Dolichandra unguis-cati* (L.)

L.G.Lohmann

Bignonia calycina DC., Prodr. 9: 160. 1845 = *Stizophyllum perforatum* (Cham.)

Miers

Bignonia candicans Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792 ≡ *Fridericia*

candicans (Rich.) L.G.Lohmann

Bignonia capensis Thunb., Prodr. Pl. Cap.: 105. 1794 ≡ *Tecoma capensis* (Thunb.)

Lindl.

Bignonia carichanensis Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland &

C.S.Kunth, Nov. Gen. Sp. Pl. 3: 137. 1818 [1819] ≡ *Fridericia carichanensis*

(Kunth) L.G.Lohmann

Bignonia caroba Vell., Fl. Flumin.: 250. 1825 [1829] ≡ *Jacaranda caroba* (Vell.)

DC.

Bignonia carolinae Lindl., Bot. Reg. 28: t. 45. 1842 ≡ *Amphilophium carolinae*

(Lindl.) L.G. Lohmann

Bignonia caryophyllea Bello, Anales Soc. Esp. Hist. Nat. 10: 293. 1881 =

Tynanthus polyanthus (Bureau ex Baill.) Sandwith

- Bignonia cassinoides* Lam., Encycl. 1: 418. 1785 ≡ *Tabebuia cassinoides* (Lam.) DC.
- Bignonia castaneifolia* (D. Don) DC., Prodr. 9: 145. 1845 ≡ *Tecoma castanifolia* (D. Don) Melch.
- Bignonia catalpa* L., Sp. Pl. 2: 622. 1753 = *Catalpa bignonioides* Walter
- Bignonia catharinae* DC., Prodr. 9: 172. 1845 = *Amphilophium crucigerum* (L.) L.G.Lohmann
- Bignonia catharinensis* Schenck, Schimp. Bot. Mittheil. 4: 191. 1892 = *Dolichandra unguis-cati* (L.) L.G.Lohmann
- Bignonia caudata* DC., Prodr. 9: 166. 1845 = *Stereospermum tetragonum* DC.
- Bignonia caudata* Miq. ex C.B.Clarke, in J.D.Hooker, Fl. Brit. India 4: 382. 1884 = *Stereospermum tetragonum* DC.
- Bignonia caudigera* S. Moore, Trans. Linn. Soc. London, Bot. II, 4: 415. 1895 ≡ *Fridericia caudigera* (S. Moore) L.G.Lohmann
- Bignonia cauliflora* Sieber ex DC., Prodr. 9: 241. 1845 = *Ophiocolea floribunda* (Bojer ex Lindl.) H. Perrier
- Bignonia chamberlaynii* Sims, Bot. Mag. 47: t. 2148. 1820 ≡ *Anemopaegma chamberlaynii* (Sims) Bureau & K. Schum.
- Bignonia chelonoides* L.f., Suppl. Pl.: 282. 1782 ≡ *Stereospermum chelonoides* (L.f.) DC.
- Bignonia cherere* Lindl., Edwards's Bot. Reg. 15: t. 1301. 1830 = *Amphilophium buccinatorium* (DC.) L.G.Lohmann
- Bignonia chica* Bonpl., in F.W.H.A.von Humboldt & A.J.A.Bonpland, Pl. Aequinoct. 1: 107. 1808 ≡ *Fridericia chica* (Bonpl.) L.G.Lohmann
- Bignonia chinensis* Lam., Encycl. 1: 423. 1785 = *Campsis grandiflora* (Thunb.) K. Schum.
- Bignonia chondrogona* Miq., Linnaea 18: 611. 1845 = *Pleonotoma clematis* (Kunth) Miers
- Bignonia chrysantha* Jacq., Pl. Hort. Schoenbr. 2: 45. 1797 ≡ *Handroanthus*

chrysanthus (Jacq.) S.O.Grose

Bignonia chrysoleuca Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 134. 1818 [1819] ≡ *Anemopaegma chrysoleucum* (Kunth) Sandwith

Bignonia cicutaria K.D.Koenig ex Mart., Denkschr. Königl. Akad. Wiss. München 6: 153. 1820 = *Millingtonia hortensis* L.f.

Bignonia ciliata Wawra, Oesterr. Bot. Z. 12: 237. 1862 = *Fridericia conjugata* (Vell.) L.G.Lohmann

Bignonia cinerea DC., Prodr. 9: 172. 1845 = *Amphilophium laxiflorum* (DC.) L.G.Lohmann

Bignonia cinnamomea DC., Prodr. 9: 164. 1845 ≡ *Fridericia cinnamomea* (DC.) L.G.Lohmann

Bignonia citrifolia Vitman, Summa Pl. 3: 511. 1789 = *Mansoa alliacea* (Lam.) A.H. Gentry

Bignonia clematis Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 141. 1818 [1819] ≡ *Pleonotoma clematis* (Kunth) Miers

Bignonia coccinea Steud., Nomencl. Bot.: 109. 1821 = *Campsis radicans* (L.) Seem.

Bignonia coccinea Vell., Fl. Flumin.: 250. 1825 [1829] = *Dolichandra cynanchoides* Cham.

Bignonia cognata Cham., Linnaea 7: 703. 1832 ≡ *Tynanthus cognatus* (Cham.) Miers

Bignonia colais Buch.-Ham. ex Dillwyn, Rev. Hortus Malab.: 28. 1839 = *Stereospermum tetragonum* DC.

Bignonia colei Bojer ex Hook., Bot. Mag. 55: t. 2817. 1828 ≡ *Colea colei* (Bojer ex Hook.) M.L.Green

Bignonia colorata Poir., in J.B.A.P.M.de Lamarck, Encycl., Suppl. 1: 634. 1811 = *Fridericia candicans* (Rich.) L.G.Lohmann

Bignonia columbiana Morong, Ann. New York Acad. Sci. 7: 186. 1892 =

Fridericia dichotoma (Jacq.) L.G.Lohmann

Bignonia comosa Cham., *Linnaea* 7: 693. 1832 ≡ *Adenocalymma comosum*
(Cham.) DC.

Bignonia compressa Lam., *Encycl.* 1: 424. 1785 = *Rhodocolea racemosa* (Lam.)
H. Perrier

Bignonia conjugata Vell., *Fl. Flumin.*: 231. 1825 [1829] ≡ *Fridericia conjugata*
(Vell.) L.G.Lohmann

Bignonia conspicua Rich. ex DC., *Prodr.* 9: 221. 1845 = *Handroanthus*
serratifolius (Vahl) S.O.Grose

Bignonia convoluta Vell., *Fl. Flumin.*: 248. 1825 [1829] ≡ *Cuspidaria convoluta*
(Vell.) A.H. Gentry

Bignonia copaia Aubl., *Hist. Pl. Guiane* 2: 650. 1775 ≡ *Jacaranda copaia* (Aubl.)
D. Don

Bignonia corallina Jacq., *Fragm. Bot.*: 37. 1800 = *Fridericia dichotoma* (Jacq.)
L.G.Lohmann

Bignonia corchoroides Cham., *Linnaea* 7: 706. 1832 ≡ *Fridericia corchoroides*
(Cham.) L.G.Lohmann

Bignonia cordata Vell., *Fl. Flumin.*: 247. 1825 [1829] ≡ *Lundia cordata* (Vell.)
DC.

Bignonia cordifolia DC., *Prodr.* 9: 162. 1845 ≡ *Manaosella cordifolia* (DC.) A.H.
Gentry

Bignonia coriacea Sellow ex Steud., *Nomencl. Bot.*, ed. 2, 1: 204. 1840 =
Tanaecium selloi (Spreng.) L.G.Lohmann

Bignonia corymbifera Vahl, *Eclog. Amer.* 2: 45. 1798 ≡ *Lundia corymbifera*
(Vahl) Sandwith

Bignonia cranalis E.H.L.Krause, *Beih. Bot. Centralbl.* 32: t. 335. 1914 =
Tabebuia pallida (Lindl.) Miers

Bignonia craterophora DC., *Prodr.* 9: 147. 1845 ≡ *Fridericia craterophora* (DC.)
L.G.Lohmann

- Bignonia crispa* Buch-Ham. ex Roxb., Fl. Ind. ed.. 1832 = *Dolichandrone atrovirens* (Roth) K. Schum.
- Bignonia crucifera* Bertol. ex DC., Prodr. 9: 213. 1845 = *Callichlamys latifolia* (Rich.) K. Schum.
- Bignonia crucigera* L., Sp. Pl. 2: 624. 1753 ≡ *Amphilophium crucigerum* (L.) L.G.Lohmann
- Bignonia cujabana* DC., Prodr. 9: 164. 1845 = *Cuspidaria sceptrum* (Cham.) L.G.Lohmann
- Bignonia cuneifolia* DC., Prodr. 9: 157. 1845 ≡ *Fridericia cuneifolia* (DC.) L.G.Lohmann
- Bignonia cuprea* Cham., Linnaea 7: 665. 1832 = *Fridericia chica* (Bonpl.) L.G.Lohmann
- Bignonia cuprea* var. *grandiflora* Cham., Linnaea 7: 666. 1832 = *Fridericia chica* (Bonpl.) L.G.Lohmann
- Bignonia cuprea* var. *parviflora* Cham., Linnaea 7: 666. 1832 = *Fridericia chica* (Bonpl.) L.G.Lohmann
- Bignonia cupulata* Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 6. 1842 = *Fridericia patellifera* (Schltdl.) L.G.Lohmann
- Bignonia curialis* Vell., Fl. Flumin.: 253. 1825 [1829] = *Jacaranda jasminoides* (Thunb.) Sandwith
- Bignonia cymbalum* Cham., Linnaea 7: 716. 1832 ≡ *Adenocalymma cymbalum* (Cham.) Bureau & K. Schum.
- Bignonia dasyantha* DC., Prodr. 9: 172. 1845 = *Tanaecium pyramidatum* (Rich.) L.G.Lohmann
- Bignonia dasyonyx* S.F.Blake, Contr. Gray Herb., n.s., 52: 93. 1917 = *Dolichandra unguis-cati* (L.) L.G.Lohmann
- Bignonia decomposita* Miq., Linnaea 18: 260. 1845 = *Cuspidaria inaequalis* (DC. ex Splitg.) L.G.Lohmann
- Bignonia densiflora* Mart. ex DC., Prodr. 9: 181. 1845 ≡ *Lundia densiflora* DC.

- Bignonia dentata* DC., Prodr. 9: 162. 1845 = *Stizophyllum perforatum* (Cham.)
Miers
- Bignonia dichotoma* Jacq., Enum. Syst. Pl.: 25. 1760 ≡ *Fridericia dichotoma*
(Jacq.) L.G.Lohmann
- Bignonia dichotoma* Vell., Fl. Flumin.: 248. 1825 [1829] = *Tanaecium selloi*
(Spreng.) L.G.Lohmann
- Bignonia difficilis* Cham., Linnaea 7: 714. 1832 ≡ *Mansoa difficilis* (Cham.)
Bureau & K. Schum.
- Bignonia digitalis* Vell., Fl. Flumin.: 251. 1825 [1829] = *Zeyheria montana* Mart.
- Bignonia digitata* E.Mey., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 12:
782. 1825 = *Tabebuia fluviatilis* (Aubl.) DC.
- Bignonia discolor* Bojer ex DC., Prodr. 9: 165. 1845 = *Ophiocolea floribunda*
(Bojer ex Lindl.) H. Perrier
- Bignonia dolichoides* Cham., Linnaea 7: 696. 1832 ≡ *Amphilophium dolichoides*
(Cham.) L.G.Lohmann
- Bignonia dombeyana* DC., Prodr. 9: 172. 1845 = *Delostoma integrifolium* D. Don
- Bignonia dubia* L., Pl. Surin.: 77. 1775 ≡ *Tabebuia dubia* (C.Wright ex Sauvalle)
Britton ex Seibert
- Bignonia echinata* Jacq., Enum. Syst. Pl.: 25. 1760 = *Amphilophium crucigerum*
(L.) L.G.Lohmann
- Bignonia echinata* Aubl., Hist. Pl. Guiane 2: 648. 1775 = *Amphilophium*
crucigerum (L.) L.G.Lohmann
- Bignonia egensis* Poepp. ex Bureau & K. Schum., in C.F.P. von Martius & auct.
suc. (eds.), Fl. Bras. 8(2): 66. 1896 ≡ *Fridericia egensis* (Poepp. ex Bureau &
K. Schum.) L.G.Lohmann
- Bignonia ehretioides* Cham., Linnaea 7: 704. 1832 = *Tanaecium pyramidatum*
(Rich.) L.G.Lohmann
- Bignonia elegans* Vell., Fl. Flumin.: 247. 1825 [1829] ≡ *Fridericia elegans* (Vell.)
L.G.Lohmann

- Bignonia elegans* Cham., *Linnaea* 7: 702. 1832 ≡ *Tynanthus elegans* Miers
- Bignonia elliptica* Thunb., *Pl. Bras.* 3: 34. 1821 = *Acanthaceae*
- Bignonia elliptica* Vell., *Fl. Flumin.*: 250. 1825 [1829] = *Jacaranda macrantha* Cham.
- Bignonia elliptica* Cham., *Linnaea* 7: 686. 1832 ≡ *Tabebuia elliptica* (DC.) Sandwith
- Bignonia elongata* Vahl, *Eclog. Amer.* 2: 45. 1798 ≡ *Amphilophium elongatum* (Vahl) L.G.Lohmann
- Bignonia erubescens* DC., *Prodr.* 9: 157. 1845 ≡ *Fridericia erubescens* (DC.) L.G.Lohmann
- Bignonia erubescens* var. *breviflora* DC., *Prodr.* 9: 158. 1845 ≡ *Fridericia erubescens* (DC.) L.G.Lohmann
- Bignonia erubescens* var. *subtruncata* DC., *Prodr.* 9: 157. 1845 ≡ *Fridericia erubescens* (DC.) L.G.Lohmann
- Bignonia euphorioides* Bojer, *Hortus Maurit.*: 219. 1837 ≡ *Stereospermum euphorioides* DC.
- Bignonia exoleta* Vell., *Fl. Flumin.*: 248. 1825 [1829] = *Dolichandra unguis-cati* (L.) L.G.Lohmann
- Bignonia exserta* DC., *Prodr.* 9: 158. 1845 = *Fridericia elegans* (Vell.) L.G.Lohmann
- Bignonia fagoides* Cham., *Linnaea* 7: 680. 1832 ≡ *Fridericia fagoides* (Cham.) L.G.Lohmann
- Bignonia falcata* Vell., *Fl. Flumin.*: 245. 1825 [1829] ≡ *Amphilophium falcatum* (Vell.) L.G.Lohmann
- Bignonia falcata* K.D.Koenig ex DC., *Prodr.* 9: 206. 1845 ≡ *Dolichandrone falcata* (Wall. ex DC.) Seem.
- Bignonia fallax* Cham., *Linnaea* 7: 717. 1832 = *Adenocalymma pubescens* (Spreng.) L.G.Lohmann
- Bignonia farinosa* Salzm. ex DC., *Prodr.* 9: 185. 1845 = *Fridericia conjugata*

(Vell.) L.G.Lohmann

Bignonia fasciculata Vell., Fl. Flumin.: 247. 1825 [1829] ≡ *Tynanthus fasciculatus* (Vell.) Miers

Bignonia ferdinandi Welw., Apont.: 584. 1859 ≡ *Fernandoa ferdinandi* (Welw.) Baill. ex K. Schum.

Bignonia filiformis A.Cunn. ex DC., Prodr. 9: 209. 1845 ≡ *Dolichandrone filiformis* (DC.) Fenzl ex F.Muell.

Bignonia fimbriata Wall. ex G. Don, Gen. Hist. 4: 221. 1837 ≡ *Stereospermum fimbriatum* (Wall. ex G. Don) DC.

Bignonia flava DC., Prodr. 9: 168. 1845 = *Adenocalymma neoflavum* L.G.Lohmann

Bignonia flavescens Vell., Fl. Flumin.: 252. 1825 [1829] = *Handroanthus serratifolius* (Vahl) S.O.Grose

Bignonia flavida DC., Prodr. 9: 168. 1845 = *Adenocalymma neoflavum* L.G.Lohmann

Bignonia floribunda Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 134. 1818 [1819] ≡ *Fridericia floribunda* (Kunth) L.G.Lohmann

Bignonia floribunda G. Don, Gen. Hist. 4: 216. 1837 ≡ *Fridericia floribunda* (Kunth) L.G.Lohmann

Bignonia florida Salisb., Prodr. Stirp. Chap. Allerton: 106. 1796 = *Campsis radicans* (L.) Seem.

Bignonia fluminensis Vell., Fl. Flumin.: 246. 1825 [1829] ≡ *Pleonotoma fluminensis* (Vell.) A.H. Gentry

Bignonia fluviatilis Aubl., Hist. Pl. Guiane 2: 655. 1775 ≡ *Tabebuia fluviatilis* (Aubl.) DC.

Bignonia fluviatilis G. Mey., Prim. Fl. Esseq.: 212. 1818 = *Tabebuia rosea* (Bertol.) Bertero ex A.DC.

Bignonia fockeana Miq., Linnaea 18: 609. 1845 = *Martinella obovata* (Kunth)

Bureau & K. Schum.

Bignonia fraxinifolia (Kunth) Spreng., Syst. Veg. 2: 833. 1825 = *Dolichandra quadrivalvis* (Jacq.) L.G.Lohmann

Bignonia frutescens Mill., Gard. Dict. ed. 8: 3. 1768 = *Tecoma stans* (L.) Juss. ex Kunth

Bignonia fulva Cav., Icon. 3: 58. 1795 ≡ *Tecoma fulva* (Cav.) G. Don

Bignonia ghorta Buch.-Ham. ex G. Don, Gen. Hist. 4: 222. 1837 ≡ *Pauldopia ghorta* (Buch.-Ham. ex G. Don) Steenis

Bignonia giesbreghtii C.Heller ex Peyr, Linnaea 30: 45. 1859 = *Amphilophium buccinatorium* (DC.) L.G.Lohmann

Bignonia glaberrima Cham., Linnaea 7: 677. 1832 = *Adenocalymma pedunculatum* (Vell.) L.G.Lohmann

Bignonia glabrata Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 135. 1818 [1819] = *Fridericia dichotoma* (Jacq.) L.G.Lohmann

Bignonia glandulosa Schum., in E.Thonning & F.C.Schumacher, Beskr. Guin. Pl.: 274. 1827 = *Newbouldia laevis* (P.Beauv.) Seem.

Bignonia glandulosa Mart., Flora 24(11) Beibl.: 27. 1841 = *Stizophyllum perforatum* (Cham.) Miers

Bignonia glandulosa Mart. ex DC., Prodr. 9: 149. 1845 = *Stizophyllum perforatum* (Cham.) Miers

Bignonia glauca Decne., in V.Jacquemont, Voy. Inde: 137. 1841 = *Tecomella undulata* (Sm.) Seem.

Bignonia glutinosa DC., Prodr. 9: 162. 1845 = *Cuspidaria sceptrum* (Cham.) L.G.Lohmann

Bignonia glutinosa var. *angustifolia* Mart. ex DC., Prodr. 9: 162. 1845 = *Cuspidaria sceptrum* (Cham.) L.G.Lohmann

Bignonia gnaphalantha A. Rich., in R. de la Sagra, Hist. Fis. Cuba, Bot. 11: 105. 1850 ≡ *Amphilophium gnaphalanthum* (A. Rich.) L.G.Lohmann

- Bignonia gracilis* Lodd., Bot. Cab. 18: t. 1705. 1831 = *Dolichandra unguis-cati* (L.) L.G.Lohmann
- Bignonia grandiflora* Thunb., Nova Acta Soc. Sci. Upsal. 4: 39. 1783 ≡ *Campsis grandiflora* (Thunb.) K. Schum.
- Bignonia grandifolia* Jacq., Pl. Hort. Schoenbr. 3: 19. 1798 ≡ *Anemopaegma grandifolium* (Jacq.) Merr. & Sandwith
- Bignonia grandifolia* Vell., Fl. Flumin.: 247. 1825 [1829] = *Adenocalymma ternatum* (Vell.) Mello ex Bureau & K. Schum.
- Bignonia gratissima* K.D.Koenig ex DC., Prodr. 9: 211. 1845 = *Stereospermum chelonoides* (L.f.) DC.
- Bignonia grewoides* S. Moore, Trans. Linn. Soc. London, Bot. 4: 413. 1895 = *Fridericia fagoides* (Cham.) L.G.Lohmann
- Bignonia guarume* Dombey ex DC., Prodr. 9: 225. 1845 = *Tecoma fulva* (Cav.) G. Don
- Bignonia haemantha* Bertol. ex Spreng., Syst. Veg. 2: 832. 1825 ≡ *Tabebuia haemantha* (Bertol. ex Spreng.) DC.
- Bignonia hebantha* Mart. ex DC., Prodr. 9: 181. 1845 = *Lundia virginalis* DC.
- Bignonia heptaphylla* Vell., Fl. Flumin.: 251. 1825 [1829] ≡ *Handroanthus heptaphyllus* (Vell.) Mattos
- Bignonia heterophylla* Willd., Sp. Pl. 3: 298. 1800 = *Pachyptera kerere* (Aubl.) Sandwith
- Bignonia heteropoda* DC., Prodr. 9: 173. 1845 = *Handroanthus ochraceus* (Cham.) Mattos
- Bignonia heterotricha* DC., Prodr. 9: 173. 1845 = *Handroanthus ochraceus* (Cham.) Mattos
- Bignonia hexagona* DC., Prodr. 9: 173. 1845 = *Amphilophium crucigerum* (L.) L.G.Lohmann
- Bignonia hibiscifolia* Cham., Linnaea 7: 705. 1832 = *Fridericia dichotoma* (Jacq.) L.G.Lohmann

- Bignonia hirsuta* Lam., Encycl. 1: 422. 1785 = *Vitex sp.*
- Bignonia hirta* Vell., Fl. Flumin.: 249. 1825 [1829] = *Fridericia mollis* (Vahl)
L.G.Lohmann
- Bignonia hispida* DC., Prodr. 9: 152. 1845 = *Fridericia artherion* (Mart.)
L.G.Lohmann
- Bignonia hondensis* Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland &
C.S.Kunth, Nov. Gen. Sp. Pl. 3: 135. 1818 [1819] = *Callichlamys latifolia*
(Rich.) K. Schum.
- Bignonia hortensis* (L.f.) Oken, Allg. Naturgesch. 3(2): 1009. 1841 ≡ *Millingtonia*
hortensis L.f.
- Bignonia hymenaea* DC., Prodr. 9: 158. 1845 ≡ *Mansoa hymenaea* (DC.) A.H.
Gentry
- Bignonia ignea* Vell., Fl. Flumin.: 244. 1825 [1829] = *Pyrostegia venusta* (Ker
Gawl.) Miers
- Bignonia ilicifolia* Pers., Syn. Pl. 2: 170. 1806 ≡ *Phyllarthron ilicifolium* (Pers.) H.
Perrier
- Bignonia imperatoris-maximiliani* Wawra, Bot. Ergebn. 73: t. 10. 1866 ≡
Adenocalymma imperatoris-maximiliani (Wawra) L.G. Lohmann
- Bignonia impressa* Rusby, Mem. Torrey Bot. Club 6: 100. 1896 [1897] ≡
Adenocalymma impressum (Rusby) Sandwith
- Bignonia inaequalis* DC. ex Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 6. 1842
≡ *Cuspidaria inaequalis* (DC. ex Splitg.) L.G.Lohmann
- Bignonia inaequalis* DC., Prodr. 9: 170. 1845 ≡ *Cuspidaria inaequalis* (DC. ex
Splitg.) L.G.Lohmann
- Bignonia incisa* DC., Prodr. 9: 224. 1845 = *Tecoma stans* (L.) Juss. ex Kunth
- Bignonia indica* L., Sp. Pl. 2: 625. 1753 ≡ *Oroxylum indicum* (L.) Kurz
- Bignonia indica* Lour., Fl. Cochinch.: 460. 1790 = *Pajanelia longifolia* (Willd.) K.
Schum.
- Bignonia inflata* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 256. 1879 =

Dolichandra unguis-cati (L.) L.G.Lohmann

Bignonia jasminifolia Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 141. 1818 [1819] ≡ *Pleonotoma jasminifolia* (Kunth) Miers

Bignonia jasminoides Thunb., Pl. Bras. 3: 36. 1821 ≡ *Jacaranda jasminoides* (Thunb.) Sandwith

Bignonia kerere Aubl., Hist. Pl. Guiane 2: 644. 1775 ≡ *Pachyptera kerere* (Aubl.) Sandwith

Bignonia labiata Cham., Linnaea 7: 701. 1832 ≡ *Tynanthus labiatus* (Cham.) Miers

Bignonia lactiflora Vahl, Symb. Bot. 3: 80. 1794 ≡ *Amphilophium lactiflorum* (Vahl) L.G.Lohmann

Bignonia laevigata Klotzsch ex Bureau & K. Schum., in C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 8(2): 113. 1896 = *Mansoa hymenaea* (DC.) A.H. Gentry

Bignonia lanata R. Br. ex Fresen., Flora 21: 607. 1838 = *Stereospermum kunthianum* Cham.

Bignonia lanata Steud., Nomencl. Bot., ed. 2, 1: 205. 1840 = *Ophiocolea floribunda* (Bojer ex Lindl.) H. Perrier

Bignonia lanceolata DC., Prodr. 9: 163. 1845 = *Anemopaegma velutinum* Mart. ex DC.

Bignonia lanuginosa Hemsl., Biol. Cemt.-Amer., Bot. 2: 491. 1882 = *Dolichandra unguis-cati* (L.) L.G.Lohmann

Bignonia laserpitiifolia Mart. ex DC., Prodr. 9: 168. 1845 = *Adenocalymma pedunculatum* (Vell.) L.G.Lohmann

Bignonia latifolia Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792 ≡ *Callichlamys latifolia* (Rich.) K. Schum.

Bignonia laurifolia Vahl, Eclog. Amer. 2: 44. 1798 = *Tanaecium pyramidatum* (Rich.) L.G.Lohmann

- Bignonia laxiflora* DC., Prodr. 9: 173. 1845 ≡ *Amphilophium laxiflorum* (DC.)
L.G.Lohmann
- Bignonia laxiflora* Poepp. ex Bureau & K. Schum., in C.F.P. von Martius & auct.
suc. (eds.), Fl. Bras. 8(2): 197. 1896 = *Tynanthus polyanthus* (Bureau ex
Baill.) Sandwith
- Bignonia lenta* Mart. ex DC., Prodr. 9: 159. 1845 = *Tanaecium pyramidatum*
(Rich.) L.G.Lohmann
- Bignonia lepidophylla* A. Rich., in R. de la Sagra, Hist. Phys. Cuba, Pl. Vasc. 11:
104. 1850 ≡ *Tabebuia lepidophylla* (A. Rich.) Greenm. ex Combs
- Bignonia lepidota* Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth,
Nov. Gen. Sp. Pl. 3: 139. 1818 [1819] ≡ *Tabebuia lepidota* (Kunth) Britton
- Bignonia leucantha* Vell., Fl. Flumin.: 251. 1825 [1829] ≡ *Sparattosperma*
leucanthum (Vell.) K. Schum.
- Bignonia leucopogon* Cham., Linnaea 7: 707. 1832 ≡ *Fridericia leucopogon*
(Cham.) L.G.Lohmann
- Bignonia leucopogona* St.-Lag., Ann. Soc. Bot. Lyon 7: 121. 1880 ≡ *Fridericia*
leucopogon (Cham.) L.G.Lohmann
- Bignonia leucoxylla* Vell., Fl. Flumin.: 252, t. 54. 1825 [1829] = *Tabebuia*
obtusifolia (Cham.) Bureau
- Bignonia leucoxyllon* L., Sp. Pl. 2: 624. 1753 = *Tabebuia heterophylla* (DC.)
Britton
- Bignonia leucoxyllon* DC., Prodr. 9: 173. 1845 = *Sparattosperma leucanthum*
(Vell.) K. Schum.
- Bignonia linearis* Cav., Icon. 3: 35. 1795 ≡ *Chilopsis linearis* (Cav.) Sweet
- Bignonia litoralis* Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth,
Nov. Gen. Sp. Pl. 3: 139. 1818 [1819] = *Fridericia mollissima* (Kunth)
L.G.Lohmann
- Bignonia longa* Vell., Fl. Flumin.: 249. 1825 [1829] = *Lundia cordata* (Vell.) DC.
- Bignonia longiflora* Vell., Fl. Flumin.: 252. 1825 [1829] = *Handroanthus vellosi*

(Toledo) Mattos

Bignonia longifolia Willd., Sp. Pl. 3: 306. 1800 ≡ *Pajanelia longifolia* (Willd.) K. Schum.

Bignonia longisiliqua Jacq., Select. Stirp. Amer. Hist.: 234. 1780 ≡ *Catalpa longissima* (Jacq.) Dum.Cours.

Bignonia longisiliqua Bertol. ex Spreng., Syst. Veg. 2: 830. 1825 = *Martinella obovata* (Kunth) Bureau & K. Schum.

Bignonia longisiliqua Vell., Fl. Flumin.: 247. 1825 [1829] = *Stizophyllum perforatum* (Cham.) Miers

Bignonia longissima Jacq., Enum. Syst. Pl.: 25. 1760 ≡ *Catalpa longissima* (Jacq.) Dum.Cours.

Bignonia longissima Lour., Fl. Cochinch.: 380. 1790 = *Dolichandrone spathacea* (L.f.) Seem.

Bignonia lugubris Salisb., Prodr. Stirp. Chap. Allerton: 106. 1796 = *Oroxylum indicum* (L.) Kurz

Bignonia lundii DC., Prodr. 9: 173. 1845 = *Amphilophium crucigerum* (L.) L.G.Lohmann

Bignonia macrophylla Cham., Linnaea 7: 689. 1832 = *Adenocalymma ternatum* (Vell.) Mello ex Bureau & K. Schum.

Bignonia macrostachya Wall. ex G. Don, Gen. Hist. 4: 22. 1837 = *Pajanelia longifolia* (Willd.) K. Schum.

Bignonia magnoliifolia Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 136. 1818 [1819] ≡ *Amphilophium magnoliifolium* (Kunth) L.G.Lohmann

Bignonia mansoana DC., Prodr. 9: 157. 1845 ≡ *Amphilophium mansoanum* (DC.) L.G.Lohmann

Bignonia marginata Cham., Linnaea 7: 695. 1832 ≡ *Adenocalymma marginatum* (Cham.) DC.

Bignonia martinii DC., Prodr. 9: 152. 1845 = *Martinella obovata* (Kunth) Bureau

& K. Schum.

Bignonia martiusiana DC., Prodr. 9: 156. 1845 = *Tanaecium pyramidatum* (Rich.)

L.G.Lohmann

Bignonia melioides S. Moore, Trans. Linn. Soc. London, Bot., II, 4: 414. 1895 ≡

Pleonotoma melioides (S. Moore) A.H. Gentry

Bignonia meonantha Link, Enum. Hort. Berol. Alt. 2: 130. 1822 = *Pandorea*

pandorana (Andrews) Steenis

Bignonia meyeniana Schauer, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur.

19(Suppl. 1): 366. 1843 = *Tecoma fulva* (Cav.) G. Don

Bignonia microcalyx var. *acuminata* Miq., Flora 25(2): 427. 1842 = *Pleonotoma*

variabilis (Jacq.) Miers

Bignonia microphylla Lam., Encycl. 1: 418. 1785 ≡ *Tabebuia microphylla* (Lam.)

Urb.

Bignonia miranda Cham., Linnaea 7: 687. 1832 = *Anemopaegma arvense* (Vell.)

Stellfeld ex De Souza

Bignonia modesta S. Moore, Trans. Linn. Soc. London, Bot. 4: 416. 1895 =

Stizophyllum riparium (Kunth) Sandwith

Bignonia mollis Vahl, Eclog. Amer. 2: 46. 1798 ≡ *Fridericia mollis* (Vahl)

L.G.Lohmann

Bignonia mollissima Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland &

C.S.Kunth, Nov. Gen. Sp. Pl. 3: 133. 1818 [1819] ≡ *Fridericia mollissima*

(Kunth) L.G.Lohmann

Bignonia moluccana DC., Prodr. 9: 144. 1845 = Verbenaceae

Bignonia moringifolia DC., Prodr. 9: 170. 1845 ≡ *Adenocalymma moringifolium*

(DC.) L.G.Lohmann

Bignonia morongii Britton, Ann. New York Acad. Sci. 7: 185. 1893 = *Tabebuia*

nodosa (Griseb.) Griseb.

Bignonia multiflora Salzm. ex DC., Prodr. 9: 160. 1845 = *Lundia cordata* (Vell.)

DC.

- Bignonia multijuga* Wall., Pl. Asiat. Rar. 1: 81. 1830 = *Pajanelia longifolia* (Willd.) K. Schum.
- Bignonia muricata* DC., Prodr. 9: 173. 1845 = *Amphilophium crucigerum* (L.) L.G.Lohmann
- Bignonia myriantha* Cham., Linnaea 7: 684. 1832 ≡ *Xylophragma myrianthum* (Cham.) Sprague
- Bignonia myriantha* Poepp. ex Bureau & K. Schum., in C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 8(2): 197. 1896 = *Tynanthus polyanthus* (Bureau ex Baill.) Sandwith
- Bignonia nematocarpa* Bojer, Hortus Maurit.: 219. 1837 ≡ *Stereospermum nematocarpum* (Bojer) DC.
- Bignonia nervosa* Dombrain ex DC., Prodr. 9: 198. 1845 = *Delostoma integrifolium* D. Don
- Bignonia nitida* Britton ex Bureau & K. Schum., in C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 8(2): 34. 1896 = *Fridericia florida* (DC.) L.G.Lohmann
- Bignonia nitidula* Mart. ex DC., Prodr. 9: 181. 1845 = *Lundia virginalis* DC.
- Bignonia nivea* Kraenzl., Bot. Jahrb. Syst. 54(119): 26. 1916 = *Amphilophium* sp.
- Bignonia nodosa* Silva Manso, Enum. Subst. Braz.: 40. 1836 ≡ *Adenocalymma nodosum* (Silva Manso) L.G.Lohmann
- Bignonia obliqua* Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 135. 1818 [1819] = *Fridericia dichotoma* (Jacq.) L.G.Lohmann
- Bignonia obovata* (Kunth) Spreng., Syst. Veg. 2: 830. 1825 ≡ *Martinella obovata* (Kunth) Bureau & K. Schum.
- Bignonia obovata* Vell., Fl. Flumin.: 251. 1825 [1829] = *Jacaranda puberula* Cham.
- Bignonia obtusifolia* Lam., Encycl. 1: 418. 1785 = *Tabebuia cassinoides* (Lam.) DC.
- Bignonia occidentalis* Salzm. ex DC., Prodr. 9: 160. 1845 = *Stizophyllum*

perforatum (Cham.) Miers

Bignonia odorata Bello, Anales Soc. Esp. Hist. Nat. 10: 293. 1881 =

Amphilophium lactiflorum (Vahl) L.G.Lohmann

Bignonia orbiculata Jacq., Enum. Syst. Pl.: 25. 1760 ≡ *Anemopaegma*

orbiculatum (Jacq.) DC.

Bignonia oxyphylla DC., Prodr. 9: 169. 1845 = *Radermachera gigantea* (Blume)

Miq.

Bignonia pajanelia Buch-Ham., Trans. Linn. Soc. London 13: 515. 1822 =

Pajanelia longifolia (Willd.) K. Schum.

Bignonia pallida Lindl., Bot. Reg. 21: t. 965. 1827 ≡ *Tabebuia pallida* (Lindl.)

Miers

Bignonia pandorana Andrews, Bot. Repos. 2: t. 86. 1799 ≡ *Pandorea pandorana*

(Andrews) Steenis

Bignonia pandorea Vent., Jard. Malmaison: t. 43. 1804 ≡ *Pandorea pandorana*

(Andrews) Steenis

Bignonia paniculata L., Sp. Pl. 2: 623. 1753 ≡ *Amphilophium paniculatum* (L.)

Kunth

Bignonia pannosa DC., Prodr. 9: 148. 1845 ≡ *Amphilophium pannosum* (DC.)

Bureau & K. Schum.

Bignonia parkeri DC., Prodr. 9: 157. 1845 ≡ *Amphilophium parkeri* (DC.)

L.G.Lohmann

Bignonia patellifera Schltdl., Linnaea 8: 516. 1833 ≡ *Fridericia patellifera*

(Schltdl.) L.G.Lohmann

Bignonia patrisiana DC., Prodr. 9: 174. 1845 = *Handroanthus serratifolius* (Vahl)

S.O.Grose

Bignonia pearcei Rusby, Mem. Torrey Bot. Club 6: 100. 1896 ≡ *Fridericia*

pearcei (Rusby) L.G.Lohmann

Bignonia pedunculata Vell., Fl. Flumin.: 250. 1825 [1829] ≡ *Adenocalymma*

pedunculatum (Vell.) L.G.Lohmann

- Bignonia pentandra* Lour., Fl. Cochinch.: 379. 1790 = *Oroxylum indicum* (L.)
Kurz
- Bignonia pentaphylla* L., Sp. Pl. ed. 2: 870. 1763 = *Tabebuia heterophylla* (DC.)
Britton
- Bignonia perforata* Cham., Linnaea 7: 667. 1832 ≡ *Stizophyllum perforatum*
(Cham.) Miers
- Bignonia perianthomega* Vell., Fl. Flumin.: 248. 1825 [1829] = *Perianthomega*
vellozoi Bureau
- Bignonia peruviana* L., Sp. Pl. 2: 625. 1753 = *Vitaceae*
- Bignonia phaseoloides* Cham., Linnaea 7: 698. 1832 = *Amphilophium crucigerum*
(L.) L.G.Lohmann
- Bignonia physaloides* Cham., Linnaea 7: 668. 1832 = *Stizophyllum perforatum*
(Cham.) Miers
- Bignonia pilulifera* Rich., Actes Soc. Hist. Nat. Paris 1: 111. 1792 ≡ *Fridericia*
pilulifera (Rich.) L.G.Lohmann
- Bignonia platydactyla* Barb.Rodr., Vellosia, ed. 2, 1: 51. 1891 = *Manaosella*
cordifolia (DC.) A.H. Gentry
- Bignonia platyphylla* Cham., Linnaea 7: 679. 1832 ≡ *Fridericia platyphylla*
(Cham.) L.G.Lohmann
- Bignonia poeppigii* DC., Prodr. 9: 174. 1845 ≡ *Fridericia poeppigii* (DC.)
L.G.Lohmann
- Bignonia populifolia* DC., Prodr. 9: 159. 1845 = *Dolichandra quadrivalvis* (Jacq.)
L.G.Lohmann
- Bignonia porteriana* Wall. ex DC., Prodr. 9: 165. 1845 = *Radermachera*
glandulosa (Blume) Miq.
- Bignonia pratensis* Poepp. ex Bureau & K. Schum., in C.F.P. von Martius & auct.
suc. (eds.), Fl. Bras. 8(2): 256. 1897 ≡ *Xylophragma pratense* (Bureau & K.
Schum.) Sprague
- Bignonia procera* Willd., Sp. Pl. 3: 307. 1800 = *Jacaranda copaia* (Aubl.) D. Don

- Bignonia pseudoquercus* Tussac, Fl. Antill. 4: 118. 1827 = *Catalpa longissima*
(Jacq.) Dum.Cours.
- Bignonia pseudounguis* Desf., Tabl. École Bot., ed. 3: 397. 1829 = *Dolichandra*
unguis-cati (L.) L.G.Lohmann
- Bignonia pterocarpa* Cham., Linnaea 7: 673. 1832 = *Cuspidaria convoluta* (Vell.)
A.H. Gentry
- Bignonia pubescens* L., Sp. Pl. ed. 2, 2: 870. 1763 ≡ *Fridericia pubescens* (L.)
L.G.Lohmann
- Bignonia pulchella* Cham., Linnaea 7: 663. 1832 ≡ *Fridericia pulchella* (Cham.)
L.G.Lohmann
- Bignonia pulchra* Cham., Linnaea 7: 708. 1832 ≡ *Cuspidaria pulchra* (Cham.)
L.G.Lohmann
- Bignonia punctata* DC., Prodr. 9: 160. 1845 = *Stizophyllum perforatum* (Cham.)
Miers
- Bignonia punicea* Mart., Herb. Fl. Bras.: 255. 1841 = *Fridericia leucopogon*
(Cham.) L.G.Lohmann
- Bignonia pyramidata* Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792 ≡ *Tanaecium*
pyramidatum (Rich.) L.G.Lohmann
- Bignonia quadrilocularis* Roxb., Pl. Coromandel 2: 24. 1799 ≡ *Heterophragma*
quadriloculare (Roxb.) K. Schum.
- Bignonia quadripinnata* Blanco, Fl. Filip.: 499. 1837 = *Oroxylum indicum* (L.)
Kurz
- Bignonia quadrivalvis* Jacq., Fragm. Bot.: 37. 1800 [1809] ≡ *Dolichandra*
quadrivalvis (Jacq.) L.G.Lohmann
- Bignonia quercus* Lam., Encycl. 1: 417. 1785 = *Catalpa longissima* (Jacq.)
Dum.Cours.
- Bignonia quinquefolia* Vell., Fl. Flumin.: 252. 1825 [1829] = *Cybistax*
antisyphilitica (Mart.) Mart.
- Bignonia racemosa* Lam., Encycl. 1: 424. 1785 ≡ *Rhodocolea racemosa* (Lam.) H.

Perrier

Bignonia radiata L., Sp. Pl. 2: 624. 1753 ≡ *Argylia radiata* (L.) D. Don

Bignonia radicans L., Sp. Pl. 2: 624. 1753 ≡ *Campsis radicans* (L.) Seem.

Bignonia radicans var. *coccinea* Pursh, Fl. Amer. Sept. 2: 420. 1814 ≡ *Campsis radicans* (L.) Seem.

Bignonia radicans var. *flammea* Pursh, Fl. Amer. Sept. 2: 420. 1814 ≡ *Campsis radicans* (L.) Seem.

Bignonia radicans var. *minor* Castigl., Verh. Bot. Vereins Prov. Brandenburg 2: 210. 1790 ≡ *Campsis radicans* (L.) Seem.

Bignonia ramiflora Decne., Nouv. Ann. Mus. Hist. Nat. 3: 381. 1834 =
Rhodocolea racemosa (Lam.) H. Perrier

Bignonia regnelliana Sond., Linnaea 22: 558. 1849 = *Fridericia platyphylla*
(Cham.) L.G.Lohmann

Bignonia rego Vell., Fl. Flumin.: 249. 1825 [1829] ≡ *Fridericia rego* (Vell.)
L.G.Lohmann

Bignonia rigescens Jacq., Pl. Hort. Schoenbr. 2: 44. 1797 = *Amphilophium lactiflorum* (Vahl) L.G.Lohmann

Bignonia riparia Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. Pl. 3: 138. 1818 [1819] ≡ *Stizophyllum riparium* (Kunth)
Sandwith

Bignonia rivularis DC., Prodr. 9: 199. 1845 = *Cybistax antisiphilitica* (Mart.)
Mart.

Bignonia rosea Pav. ex DC., Prodr. 9: 174. 1845 = *Delostoma dentatum* D. Don

Bignonia rosea DC., Prodr. 9: 174. 1845 = *Fridericia chica* (Bonpl.)
L.G.Lohmann

Bignonia roseoalba Ridl., J. Linn. Soc., Bot. 27: 52. 1890 ≡ *Tabebuia roseoalba*
(Ridl.) Sandwith

Bignonia rotundata DC., Prodr. 9: 163. 1845 = *Fridericia dichotoma* (Jacq.)
L.G.Lohmann

- Bignonia rubescens* S. Moore, Trans. Linn. Soc. London, Bot. 4: 412. 1895 =
Fridericia chica (Bonpl.) L.G.Lohmann
- Bignonia rufescens* DC., Prodr. 9: 174. 1845 = *Fridericia chica* (Bonpl.)
L.G.Lohmann
- Bignonia rufinervis* Mart., Flora 24(11) Beibl.: 28. 1841 = *Callichlamys latifolia*
(Rich.) K. Schum.
- Bignonia rugosa* Schltld., Linnaea 26: 656. 1855 ≡ *Anemopaegma rugosum*
(Schltld.) Sprague
- Bignonia rupestris* Gardner, London J. Bot. 1: 179. 1842 = *Tanaecium*
pyramidatum (Rich.) L.G.Lohmann
- Bignonia rusbyi* Britton ex Rusby, Bull. Torrey Bot. Club 27: 71. 1900 =
Amphilophium magnoliifolium (Kunth) L.G.Lohmann
- Bignonia salicifolia* Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland &
C.S.Kunth, Nov. Gen. Sp. Pl. 3: 133. 1818 [1819] ≡ *Anemopaegma*
salicifolium (Kunth) Sandwith
- Bignonia salicifolia* Sessé & Moc., Pl. Nov. Hisp.: 99. 1889 = *Astianthus*
viminalis (Kunth) Baill.
- Bignonia salzmännii* DC., Prodr. 9: 174. 1845 ≡ *Adenocalymma salzmännii* DC.
- Bignonia samydoides* Cham., Linnaea 7: 669. 1832 ≡ *Fridericia samydoides*
(Cham.) L.G.Lohmann
- Bignonia scandens* Vell., Fl. Flumin.: 246. 1825 [1829] = *Anemopaegma*
chamberlaynii (Sims) Bureau & K. Schum.
- Bignonia sceptrum* Cham., Linnaea 7: 710. 1832 ≡ *Cuspidaria sceptrum* (Cham.)
L.G.Lohmann
- Bignonia selloi* Spreng., Syst. Veg. 2: 831. 1825 ≡ *Tanaecium selloi* (Spreng.)
L.G.Lohmann
- Bignonia serrata* Pav. ex G. Don, Gen. Hist. 4: 228. 1837 = *Tecoma castanifolia*
(D. Don) Melch.
- Bignonia serratifolia* Vahl, Eclog. Amer. 2: 46. 1798 ≡ *Handroanthus*

serratifolius (Vahl) S.O.Grose

Bignonia serratula Wall. ex DC., Prodr. 9: 206. 1845 = *Dolichandrone serrulata*
(Wall. ex DC.) Seem.

Bignonia serrulata Wall. ex DC., Biblioth. Universelle Genève 17: 124. 1838 ≡
Dolichandrone serrulata (Wall. ex DC.) Seem.

Bignonia sieberi DC., Prodr. 9: 174. 1845 = *Fridericia pubescens* (L.)
L.G.Lohmann

Bignonia simplex A. Rich., in R. de la Sagra, Hist. Phys. Cuba, Pl. Vasc. 11: 104.
1850 = *Fridericia podopogon* (DC.) L.G.Lohmann

Bignonia simplicifolia Pav. ex DC., Prodr. 9: 198. 1845 = *Delostoma integrifolium*
D. Don

Bignonia sinclairii Benth., Bot. Voy. Sulphur: 129. 1845 = *Tanaecium*
pyramidatum (Rich.) L.G.Lohmann

Bignonia sorbifolia Salisb., Prodr. Stirp. Chap. Allerton: 106. 1796 = *Tecoma*
stans (L.) Juss. ex Kunth

Bignonia spathacea L.f., Suppl. Pl.: 283. 1782 ≡ *Dolichandrone spathacea* (L.f.)
Seem.

Bignonia spathacea Roxb., Pl. Coromandel 2: 24. 1799 = *Dolichandrone falcata*
(Wall. ex DC.) Seem.

Bignonia spectabilis Salisb., Prodr. Stirp. Chap. Allerton: 106. 1796 = *Catalpa*
bignonioides Walter

Bignonia squalus Vell., Fl. Flumin.: 290. 1825 [1829] = *Amphilophium*
crucigerum (L.) L.G.Lohmann

Bignonia squamellulosa DC., Prodr. 9: 174. 1845 = *Tabebuia aurea* (Silva
Manso) Benth. & Hook.f. ex S. Moore

Bignonia staminea Lam., Encycl. 1: 421. 1785 ≡ *Amphilophium stamineum*
(Lam.) L.G.Lohmann

Bignonia stans L., Sp. Pl. ed. 2: 871. 1763 ≡ *Tecoma stans* (L.) Juss. ex Kunth

Bignonia stipulata (Wall.) Roxb., Fl. Ind. ed.. 1832 ≡ *Markhamia stipulata* (Wall.)

Seem.

Bignonia stricta Klotzsch, in R.Schomburgk, Reis. Br.-Guiana 3: 969. 1848 =
Lundia densiflora DC.

Bignonia suaveolens Roxb., Fl. Ind. ed.. 1832 = *Stereospermum chelonoides* (L.f.)
DC.

Bignonia suberosa Roxb., Pl. Coromandel 3: 11. 1811 = *Millingtonia hortensis*
L.f.

Bignonia subvernica DC., Prodr. 9: 220. 1845 = *Sparattosperma leucanthum*
(Vell.) K. Schum.

Bignonia tabebuia Vell., Fl. Flumin.: 251. 1825 [1829] = *Tabebuia cassinoides*
(Lam.) DC.

Bignonia tecoma Wehmer, Pfl.-Stoffe, ed. 2, 2: 1134. 1931 = *Tecoma stans* (L.)
Juss. ex Kunth

Bignonia tecomiflora Rusby, Mem. Torrey Bot. Club 6: 101. 1896 = *Pyrostegia*
venusta (Ker Gawl.) Miers

Bignonia tecomoides DC., Prodr. 9: 166. 1845 = *Tecoma stans* (L.) Juss. ex Kunth

Bignonia telfairiae Bojer ex Hook., Bot. Mag. 57: t. 2976. 1830 ≡ *Rhodocolea*
telfairiae (Bojer ex Hook.) H. Perrier

Bignonia tenuiflora DC., Prodr. 9: 166. 1845 ≡ *Tecoma tenuiflora* (DC.) Fabris

Bignonia tenuisiliqua Vahl, Eclog. Amer. 2: 43. 1798 = *Catalpa longissima*
(Jacq.) Dum.Cours.

Bignonia ternata Vell., Fl. Flumin.: 246. 1825 [1829] ≡ *Adenocalymma ternatum*
(Vell.) Mello ex Bureau & K. Schum.

Bignonia tetragona Wall. ex DC., Prodr. 9: 211. 1845 ≡ *Stereospermum*
tetragonum DC.

Bignonia tetragonocaulis DC., Prodr. 9: 169. 1845 = *Pleonotoma jasminifolia*
(Kunth) Miers

Bignonia tetragonoloba Jacq., Fragm. Bot.: 36. 1800 ≡ *Tanaecium*
tetragonolobum (Jacq.) L.G.Lohmann

- Bignonia tetraquetra* Cham., *Linnaea* 7: 675. 1832 ≡ *Pleonotoma tetraquetra*
(Cham.) Bureau
- Bignonia thyrsoidea* DC., *Prodr.* 9: 158. 1845 = *Fridericia chica* (Bonpl.)
L.G.Lohmann
- Bignonia tiliifolia* Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth,
Nov. Gen. Sp. Pl. 3: 136. 1818 [1819] = *Amphilophium crucigerum* (L.)
L.G.Lohmann
- Bignonia tomentella* S. Moore, *Trans. Linn. Soc. London, Bot.* 4: 413. 1895 =
Fridericia pubescens (L.) L.G.Lohmann
- Bignonia tomentosa* Thunb., *Nova Acta Soc. Sci. Upsal.* 4: 39. 1783 =
Paulowniaceae Bignonia tomentosa Rich., *Actes Soc. Hist. Nat. Paris* 1: 110.
1792 = *Fridericia mollis* (Vahl) L.G.Lohmann
- Bignonia tomentosa* Pav. ex DC., *Prodr.* 9: 219. 1845 = *Handroanthus ochraceus*
(Cham.) Mattos
- Bignonia triantha* DC., *Prodr.* 9: 148. 1845 = *Dolichandra unguis-cati* (L.)
L.G.Lohmann
- Bignonia trichoclada* DC., *Prodr.* 9: 158. 1845 ≡ *Adenocalymma trichocladum*
(DC.) L.G.Lohmann
- Bignonia trifoliata* Vell., *Fl. Flumin.*: 245. 1825 [1829] ≡ *Adenocalymma*
trifoliatum (Vell.) R.C.Laroche
- Bignonia triphylla* L., *Sp. Pl. ed. 2:* 870. 1763 ≡ *Lundia triphylla* (L.)
L.G.Lohmann
- Bignonia triphylla* Willd. ex DC., *Prodr.* 9: 151. 1845 = *Fridericia chica* (Bonpl.)
L.G.Lohmann
- Bignonia tripinnata* Noronha, *Verh. Batav. Genootsch. Kunsten* 5(4): 8. 1790 =
Oroxylum indicum (L.) Kurz
- Bignonia triplinervia* Mart. ex DC., *Prodr.* 9: 153. 1845 ≡ *Fridericia triplinervia*
(Mart. ex DC.) L.G.Lohmann
- Bignonia triternata* Steud., *Nomencl. Bot., ed. 2, 1:* 205. 1840 = *Cuspidaria*
inaequalis (DC. ex Splitg.) L.G.Lohmann

Bignonia tropaeolum Jacquem. ex DC., Prodr. 9: 223. 1845 = *Tecomella undulata*
(Sm.) Seem.

Bignonia tuberculata Roxb. ex DC., Prodr. 9: 177. 1845 = *Oroxylum indicum* (L.)
Kurz

Bignonia tuberculosa Vell., Fl. Flumin.: 251. 1825 [1829] ≡ *Zeyheria tuberculosa*
(Vell.) Bureau ex Verl.

Bignonia tubulosa Klotzsch, in R.Schomburgk, Reis. Br.-Guiana 3: 969. 1848 =
Pyrostegia venusta (Ker Gawl.) Miers

Bignonia tulipifera Schum., in E.Thonning & F.C.Schumacher, Beskr. Guin. Pl.:
273. 1827 = *Spathodea campanulata* P.Beauv.

Bignonia tweediana Lindl., Bot. Reg. 26: t. 45. 1840 = *Dolichandra unguis-cati*
(L.) L.G.Lohmann

Bignonia uliginosa Gomes, Observ. Bot.-Med. Nonnullis Bras. Pl. 2: 7. 1803 =
Tabebuia cassinoides (Lam.) DC.

Bignonia umbrosa Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland &
C.S.Kunth, Nov. Gen. Sp. Pl. 3: 138. 1818 [1819] = *Lundia corymbifera*
(Vahl) Sandwith

Bignonia uncata Andrews, Bot. Repos. 8: t. 530. 1808 ≡ *Dolichandra uncata*
(Andrews) L.G.Lohmann

Bignonia uncata Sims, Bot. Mag. 37: t. 1511. 1812 ≡ *Dolichandra uncata*
(Andrews) L.G.Lohmann

Bignonia uncinata G. Mey., Prim. Fl. Esseq.: 210. 1818 = *Dolichandra uncata*
(Andrews) L.G.Lohmann

Bignonia undulata Sm., Exot. Bot. 1: 35. 1804 ≡ *Tecomella undulata* (Sm.) Seem.

Bignonia unguiculata Vell., Fl. Flumin.: 248. 1825 [1829] ≡ *Dolichandra*
unguiculata (Vell.) L.G.Lohmann

Bignonia unguiculata St.-Lag., Ann. Soc. Bot. Lyon 7: 121. 1880 ≡ *Dolichandra*
unguiculata (Vell.) L.G.Lohmann

Bignonia unguis L., Syst. Nat. 10(2): 1114. 1759 ≡ *Dolichandra unguis-cati* (L.)

L.G.Lohmann

Bignonia unguis Vell., Fl. Flumin.: 248. 1825 [1829] ≡ *Dolichandra unguis-cati*
(L.) L.G.Lohmann

Bignonia unguis var. *gracilis* (Lodd.) DC., Prodr. 9: 146. 1845 ≡ *Dolichandra*
unguis-cati (L.) L.G.Lohmann

Bignonia unguis-cati L., Sp. Pl. 2: 623. 1753 ≡ *Dolichandra unguis-cati* (L.)
L.G.Lohmann

Bignonia unguis-cati var. *exoleta* (Vell.) Sprague, Bull. Herb. Boissier, II, 5: 84.
1905 ≡ *Dolichandra unguis-cati* (L.) L.G.Lohmann

Bignonia unguis-cati var. *guatemalensis* K.Schum. & Loes., Bot. Jahrb. Syst. 23:
130. 1896 ≡ *Dolichandra unguis-cati* (L.) L.G.Lohmann

Bignonia unguis-cati var. *radicans* DC., Prodr. 9: 146. 1845 ≡ *Dolichandra*
unguis-cati (L.) L.G.Lohmann

Bignonia unguis-cati var. *serrata* Bureau & K.Schum., in C.F.P. von Martius &
auct. suc. (eds.), Fl. Bras. 8(2): 283. 1896 ≡ *Dolichandra unguis-cati* (L.)
L.G.Lohmann

Bignonia variabilis Jacq., Pl. Hort. Schoenbr. 2: 45. 1797 ≡ *Pleonotoma variabilis*
(Jacq.) Miers

Bignonia variabilis Mart., Herb. Fl. Bras.: 256. 1841 = *Fridericia samydoides*
(Cham.) L.G.Lohmann

Bignonia varians DC., Prodr. 9: 149. 1845 = *Fridericia samydoides* (Cham.)
L.G.Lohmann

Bignonia velutina DC., Prodr. 9: 162. 1845 = *Stizophyllum perforatum* (Cham.)
Miers

Bignonia venusta Ker Gawl., Bot. Reg. 3: t. 249. 1801 ≡ *Pyrostegia venusta* (Ker
Gawl.) Miers

Bignonia verrucifera Schltld., Linnaea 26: 655. 1855 ≡ *Mansoa verrucifera*
(Schltld.) A.H. Gentry

Bignonia verrucosa Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland &

C.S.Kunth, Nov. Gen. Sp. Pl. 3: 137. 1818 [1819] = *Fridericia carichanensis*
(Kunth) L.G.Lohmann

Bignonia vespertilia Barb.Rodr., Vellozia 1: 1888 = *Dolichandra unguis-cati* (L.)
L.G.Lohmann

Bignonia villosa Bertero ex Spreng., Syst. Veg. 2: 830. 1825 = *Fridericia*
dichotoma (Jacq.) L.G.Lohmann

Bignonia viminalis Kunth, in F.W.H.von Humboldt, A.J.A.Bonpland &
C.S.Kunth, Nov. Gen. Sp. Pl. 3: 132. 1818 [1819] ≡ *Astianthus viminalis*
(Kunth) Baill.

Bignonia virginalis Mart. ex DC., Prodr. 9: 181. 1845 ≡ *Lundia virginalis* DC.

Bignonia vitalba Cham., Linnaea 7: 699. 1832 = *Amphilophium crucigerum* (L.)
L.G.Lohmann

Bignonia vitalba var. *aequinoctialis* Cham., Linnaea 7: 699. 1832 =
Amphilophium crucigerum (L.) L.G.Lohmann

Bignonia vitalba var. *extratropica* Cham., Linnaea 7: 699. 1832 = *Amphilophium*
crucigerum (L.) L.G.Lohmann

Bignonia xanthinum Mart. ex Bureau, Vidensk. Meddel. Naturhist. Foren.
Kjøbenhavn 1983: 3. 1894 = *Mansoa lanceolata* (DC.) A.H. Gentry

Bignonia xylocarpa Roxb., Fl. Ind. ed.. 1832 ≡ *Radermachera xylocarpa* (Roxb.)
Roxb. ex K. Schum.

Clytostoma punctatum Bureau ex Glaziou, Bull. Soc. Bot. France 58(Mem. 3f):
526. 1911 = *Mansoa difficilis* (Cham.) Bureau & K. Schum.

Clytostoma uniflorum K. Schum., in C.F.P. von Martius & auct. suc. (eds.), Fl.
Bras. 8(2): 408. 1897 = *Mansoa difficilis* (Cham.) Bureau & K. Schum.

Cydista difficilis (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 192. 1863 ≡
Mansoa difficilis (Cham.) Bureau & K. Schum.

Cydista praepensa Miers, Proc. Roy. Hort. Soc. London 3: 190. 1863 = *Mansoa*
difficilis (Cham.) Bureau & K. Schum.

Micropaegma cupulatum (Splitg.) Pichon, Bull. Soc. Bot. France 92: 225. 1945

- [1946] = *Fridericia patellifera* (Schltdl.) L.G.Lohmann
- Mussatia caudiculata* (Standl.) Seibert, Publ. Carnegie Inst. Wash. 522: 418. 1940
 ≡ *Tanaecium caudiculatum* (Standl.) L.G.Lohmann
- Mussatia venezuelensis* Bureau, Bull. Soc. Bot. France. 1866 = *Tanaecium
 pyramidatum* (Rich.) L.G.Lohmann
- Osmhydrophora ovata* (Bureau & K. Schum.) Barb. Rodr., Pl. Jard. Rio de Janeiro
 5: 32. 1896 = *Adenocalymma schomburgkii* (DC.) L.G.Lohmann
- Phryganocydia antisiphilitica* Mart. ex DC., Prodr. 9: 199. 1845 ≡ *Cybistax
 antisiphilitica* (Mart.) Mart.
- Phryganocydia brevicalyx* Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 261.
 1929 = *Fridericia podopogon* (DC.) L.G.Lohmann
- Phryganocydia candolleana* Mart. ex DC., Prodr. 9: 207. 1845 ≡ *Neojobertia
 candolleana* (Mart. ex DC.) Bureau & K. Schum.
- Phryganocydia japurensis* Mart. ex DC., Prodr. 9: 214. 1845 ≡ *Fridericia
 japurensis* (DC.) L.G.Lohmann
- Phryganocydia longa* Mart. ex DC., Prodr. 9: 181. 1845 = *Lundia cordata* (Vell.)
 DC.
- Phryganocydia pisoniana* Mart. ex DC., Prodr. 9: 209. 1845 = *Dolichandra
 quadrivalvis* (Jacq.) L.G.Lohmann
- Phryganocydia xanthophylla* Mart. ex DC., Prodr. 9: 214. 1845 ≡ *Tanaecium
 xanthophyllum* (DC.) L.G.Lohmann
- Saritaeta triplinervia* (Mart. ex DC.) Dugand, Caldasia 3: 266. 1945 ≡ *Fridericia
 triplinervia* (Mart. ex DC.) L.G.Lohmann

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Capítulo 3

Primers for phylogeny reconstruction in Bignoniaceae (Bignoniaceae) using herbarium samples

Publicado em:

Applications in Plant Sciences 2013 1(9): 1300018

doi:10.3732/apps.1300018

Primers for phylogeny reconstruction in Bignoniaeae (Bignoniaceae) using herbarium samples¹

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Acknowledgments:

The authors thank FAPESP for scholarships to ARZ (2011/09160-5) and LHMF (2009/12508-3), and two research grants to LGL (2011/50859-2 and 12/50260-6). We also thank CNPq for a Pq-2 grant to LGL. We are extremely grateful to the Missouri Botanical Garden for authorizing DNA extraction from selected specimens.

ABSTRACT

- *Premise of the study:* New primers were developed for Bignonieae to enable phylogenetic studies within this clade using herbarium samples.
- *Methods and Results:* Internal primers were designed based on available sequences of the plastid *ndhF* gene and the *rpl32-trnL* intergenic spacer region, and the nuclear gene *PepC*. The resulting primers were used to amplify DNA extracted from herbarium materials. High quality data was obtained from herbarium samples up to 53 years old.
- *Conclusions:* The standardized methodology allows the inclusion of herbarium materials as alternative sources for phylogenetic studies throughout Bignonieae.

Key words: Bignonieae; herbarium specimens; *ndhF*; *PepC*; phylogeny; *rpl32-trnL* spacer

INTRODUCTION

The tribe Bignonieae includes 393 Neotropical species (Lohmann and Taylor, in press), representing almost half of the species in the Bignoniaceae. The tribe is mainly composed of lianas and shrubs with widespread or highly endemic distribution patterns (Lohmann & Taylor, in press).

The first molecular phylogenetic study for the tribe (Lohmann, 2006) was mainly based on recently collected samples that did not present any problems for the amplification of large DNA fragments. However, approximately 10% of the currently recognized species of Bignonieae (37 of the 392) are highly endemic and were not encountered in the field. For those species, only five or fewer herbarium samples are available (Lohmann, unpublished data), making those specimens the only source of DNA material for phylogenetic studies.

Here, we propose new primers and protocols that allow the amplification of medium-sized DNA fragments (~500 bp) from herbarium samples. The novel protocols here proposed are critical for the inclusion of rare and poorly known species of Bignonieae into a comprehensive phylogeny of the whole tribe.

METHODS AND RESULTS

DNA extraction. Total DNA of six herbarium samples (dating up to 53 years old) were extracted with Invisorb Plant Mini Kit (Invitex, Berlin, Germany). The manufacturer's protocol was followed, changing only the final step: 50 μ L of Elution Buffer was used instead of 200 μ L, as suggested by the manufacturer.

Primer development. Selected sequences of the plastid *ndhF* and nuclear *PepC* genes for Bignonieae from Lohmann (2006) were combined with newly generated sequences for the plastid *rpl32-trnL* intergenic spacer region following Shaw et al. (2007). Vouchers and GenBank accessions of the sequences used and/or generated in this paper are presented in Appendix 1. The datasets corresponding to the individual data partitions were aligned in Geneious 5.4 (Drummond et al., 2010) using the algorithm Muscle (Edgar, 2004). A thorough search for primer pairs was also conducted in Geneious, using the software Primer3 (Rozen & Skaletsky, 2000). The objective of this search was to design primers placed in highly conserved regions that would only amplify medium sized fragments (~500 bp) and would overlap adjacent

amplicons (~70 bp). Given that the nuclear marker *PepC* is present in multiple copies, with variable sizes (*PepC*-small and *PepC*-Large according to Lohmann, 2006), we focused on the amplification of *PepC*-Large, which covers all of intron 4 and holds 85% of the informative sites (Lohmann, 2006). In total, seventeen primers were initially developed (Table 1).

DNA amplifications, cloning and sequencing. PCR conditions were optimized using a common 25 μ L master mix containing the following ingredients: 5 μ L of 5X Buffer, 2.5 μ L of $MgCl_2$ (25mM), 1 μ L of dNTP (10mM), 0.5 μ L of BSA (New England Biolabs, Ipswich, USA), 0.5 μ L of each primer (10 μ M), 1 unit of GoTaq Hot Start Polymerase (Promega, Maddison, USA) and 1 μ L of genomic DNA. For the *PepC* mix, 0.25 μ L of DMSO (Sigma-Aldrich, St. Louis, USA) was also added. A standard PCR program was implemented as follows: one initial step at 95°C for 5 min, 40 cycles at 95°C for 30 sec, 48°-56°C for 30 sec and 72°C for 30 sec to 2 min; and a final step at 72°C for 10 min. The specific annealing temperature and elongation time for each primer pair is presented in Table 2.

The optimized PCR conditions were applied using the common mix. For *ndhF* and *rpl32-trnL*, products were purified by adding 1.5 μ L of Illustra ExoStar (GE, Buckinghamshire, UK) and submitting the samples to the thermal treatment as indicated by the manufacturer, with an additional step of 62° over 15 min to renature the DNA. For *PepC*, PCR products were purified with the Illustra GFX™ Purification kit (GE, Buckinghamshire, UK), due to the presence of primer dimer, and then used in a ligation protocol with pGEM® Easy Vector System (Promega, Maddison, USA). JM109 Competent *E. coli* cells (Promega, Maddison, USA) were used for the heat-shock transformation protocol. After incubation, transformant colonies were resuspended in 10 μ L of 0.5 X TE buffer and boiled for 10 min in a thermocycler. Up to 4 colonies were amplified using M13 primers and the common mix adjusted to final volume of 10 μ L. These amplifications used an initial step of 95°C for 5 min; 30 cycles of 95°C for 45 sec, 53°C for 1 min and 72°C for 90 sec and a final step of 72°C for 10 min. PCR products were purified with 0.7 μ L Illustra ExoStar.

All samples were sequenced at Macrogen Inc. (Seoul, Korea), assembled in Geneious 5.4 and deposited in GenBank (Appendix 1). Sequences annotations for *ndhF* and *PepC* follow Lohmann (2006) and annotations for the newly generated sequences of *rpl32-trnL* were established using the complete plastid genomes of

Nicotiana sylvestris (NC_007500) and *Olea europaea* (NC_013707) available in GenBank. All cloned sequences were screened for vector contamination by comparison with UniVec Database (Kitts et al. 2011) prior the submission to GenBank. Species names follow Lohmann and Taylor (in press).

The three selected molecular markers (*ndhF*, *PepC*, and *rpl32-trnL*) were successfully amplified from herbarium materials using the newly developed primer sets and proposed protocols. High quality DNA sequences were obtained for most samples (55 of 62 sequenced fragments). In the rare cases in which low-quality sequences were generated, additional PCR optimizations were conducted, none of which led to higher-quality products. In those cases, a second PCR, using 0.5 μ L of the unpurified product from the first PCR as template and the same PCR program, was adopted, leading to higher-quality products. With these optimizations, all fragments were successfully amplified and also led to high-quality sequences for *ndhF* and *PepC*. For the *rpl32-trnL* marker, the presence of two homopolymeric regions (polyA or polyT) was responsible for DNA polymerase slippage. As a result, low-quality sequences were seldom obtained immediately after this region (three of 13 sequences). To produce fully double-covered sequences, four primers (146R, 241F, 619R, and 682F; Table 1) were designed flanking the homopolymers. After these adjustments, high-quality sequences were produced for all samples. This protocol is already being used to reconstruct generic-level phylogenies in Bignoniaceae and has proved to be highly efficient in all of the 18 genera it has been tested on (Zuntini and Lohmann, in prep.; Fonseca and Lohmann, in prep.; Medeiros and Lohmann, in prep.; Calió, Winkworth, and Lohmann, in prep.).

CONCLUSIONS

The 21 new primers here proposed, combined with the eight previously available primers and optimized protocols, led to high quality sequences for the three selected molecular markers (*ndhF*, *PepC*, and *rpl32-trnL*). Those results demonstrate that herbarium materials can provide an excellent source of information for molecular phylogenetic studies in the plant family Bignoniaceae. These primers are now being used to obtain a comprehensive phylogeny for the whole tribe (Lohmann et al, in prep.). Given that the primers designed here were positioned in conserved regions, we

believe that those primers will also yield high quality sequences in other clades of the Bignoniaceae and other closely related families.

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Table 1. Primer sequences and references.

Region	Primer	Sequence	Reference
<i>ndhF</i>	5F	5'- ATG GAA CAG ACA TAT CAA TAT GSG TGG -3'	Olmstead & Sweere, 1995
	1318R	5'- CGA AAC ATA TAA AAT GCR GTT AAT CC -3'	Olmstead & Sweere, 1994
	972F	5'- GTC TCA ATT GGG TTA TAT GAT G -3'	Olmstead & Sweere, 1994
	3R	5'- CCC YAS ATA TTT GAT ACC TTC KCC G - 3	Olmstead & Sweere, 1995
	370F	5'- TTC CAT GTT GGG ATT AGT TAC TAG C -3'	This paper
	478R	5'- AGG TCG TGT GAA CCA AAA CC -3'	This paper
	741F	5'- AGG GAC CCA CYC CTA TTT CGG CT -3'	This paper
	808F	5'- AGC TCG CCT TCT TCC TCT TT -3'	This paper
	849R	5'- GGC CTA TCA AAG AGA TAA AAT TCA -3'	This paper
	1290F	5'- CAG CAG GAT TAA CCG CAT TT -3'	This paper
	1336R	5'- CGT TTA AAT GCC CCT CAA AA - 3	This paper
	1393R	5'- AGG GGT ATT TTG GCT GCC ACT GT -3'	This paper
	1680F	5'- TTG GAT CCC TAG GAA TTY CTT TT -3'	This paper
	1835R	5'- CGC TAA AAA TAT TCCG AAA TAA GC -3'	This paper
	2117R	5'- GAA ACT CAT AAT ACC AAC CCC ATT -3'	This paper
<i>rpl32-trnL</i>	trnL ^(UAG)	5'- CTG CTT CCT AAG AGC AGC GT -3'	Shaw et al, 2007
	rpl32-F	5'- CAG TTC CAA AA A AAC GTA CTT C -3'	Shaw et al, 2007
	trnL_479R	5'- TAG AAG GGC GGA TAG AAA ATC T -3'	This paper
	trnL_365F	5'- TGC CTG GAT TGA TGG YGA GAG A -3'	This paper
	trnL_407F	5'- AGA AGA CTT CAG AGA AAA TTC AAA A -3'	This paper
	rpl32_146R	5'- TCG GTA AGG TAA ACA GAA GAA -3'	This paper
	rpl32_241F	5'- ATC ATT TCC AAG CCG AGG A -3'	This paper
	rpl32_619R	5'- TTC TTT TAA TGA ACT GTT TTT GA -3'	This paper
	rpl32_682F	5'- CGG ACG ATC GAG TTT TAC AAG AGT -3'	This paper
<i>PepC</i>	4F	5'- ACT CCA CAG GAT GAG ATG AG -3'	Ayres et al, 2009
	5R	5'- GCA GCC ATC ATT CTA GCC AA -3'	Ayres et al, 2009
	IV_119F	5'- ACG RCG TGT YGA CAC TGC TYT GA -3'	This paper
	IV_197F	5'- RTC CTG GAT GGG DGG GGA TCG KG -3'	This paper
	V_25R	5'- ACT TCA GGR GTT ACC CTA GGA TTG C -3'	This paper

Table 2. Optimized PCR conditions.

Region	Primer F	Primer R	Annealing temperature (°C)	Elongation duration
<i>ndhF</i>	5F	1318R	48	2 min
	972F	3R	48	2 min
	5F	478R	52	45 sec
	370F	849R	56	45 sec
	741F	1393R	52	45 sec
	808F	1336R	55	45 sec
	1290F	1835R	51	45 sec
	1680F	2117R	50	45 sec
<i>rpl32-trnL</i>	trnL ^(UAG)	rpl32-F	48	2 min
	trnL ^(UAG)	479R	48	1 min
	407F / 365F	rpl32-F	48	1 min
<i>PepC</i>	4F	5R	48	1 min
	IV_119F	V_25R	48	1 min
	IV_197F	V_25R	48	1 min

Appendix 1. Vouchers and GenBank accessions: Species; Voucher (Herbarium), *ndhF*, *rp132-trnL*, *PepC* clones. Asterisks indicate sequences generated in this work.

Amphilophium bauhinioides (Bureau ex Baill.) L. G. Lohmann (ined.; Lohmann and Taylor, in press); Lohmann 655 (CVRD, MO), DQ222586, KC914599*, DQ222734. *Anemopaegma robustum* Bureau & K. Schum.; Assunção 126 (INPA, MO), DQ222538, KC914598*, DQ222663. *Bignonia bracteomana* (K. Schum. ex Sprague) L. G. Lohmann (ined.; Lohmann and Taylor, in press); Woytkowski 5637 (MO), KC914588*, KC914594*, KC914610*, KC914611*, KC914612*. *Bignonia convolvuloides* (Bureau & K. Schum.) L. G. Lohmann (ined.; Lohmann and Taylor, in press); Carvalho 2 (SPF), KC914586*, KC914592*, KC914605*, KC914606*, KC914607*; Gomes 278 (SPF), KC914591*, KC914597*, KC914617*, KC914618*, KC914619*. *Bignonia hyacinthina* (Standl.) L. G. Lohmann; Lohmann 642 (MO, MOL), DQ222614, KC914602*, DQ222775. *Bignonia potosina* (K. Schum. & Loes.) L. G. Lohmann (ined.; Lohmann and Taylor, in press); Álvarez 5353 (MO), KC914587*, KC914593*, KC914608*, KC914609*; Carnevali 6840 (MO), KC914590*, KC914596*, KC914614*, KC914615*, KC914616*. *Bignonia uleana* (Kraenzl.) L. G. Lohmann (ined.; Lohmann and Taylor, in press); Lohmann 617 (MO, MOL), DQ222572, KC914601*, DQ222709; Nee 39466 (MO, NY, TEX), KC914589*, KC914595*, KC914613*. *Dolichandra unguis-cati* (L.) L. G. Lohmann; Lombardi 2432 (BHCB, MO), DQ222595, KC914603*, DQ222749. *Fridericia speciosa* Mart.; Lombardi 2521 (BHCB, MO), DQ222584, KC914604*, DQ222730. *Mansoa difficilis* (Cham.) Bureau & K. Schum.; Lohmann 662 (CVRD, MO), DQ222598, KC914600*, DQ222752.

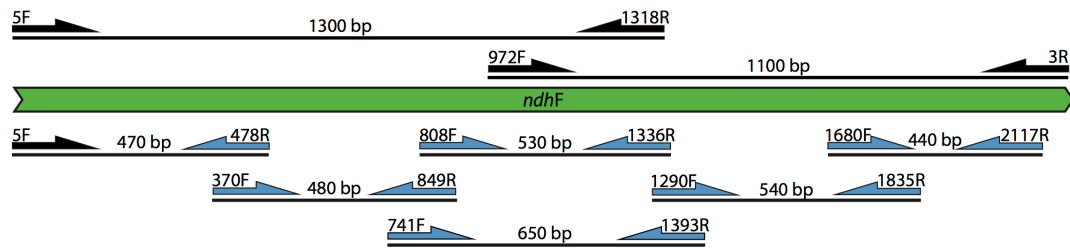
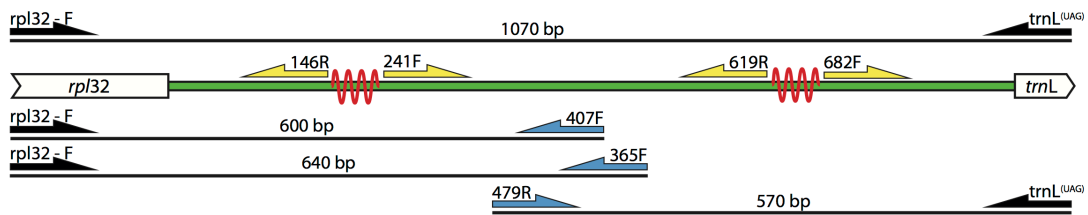
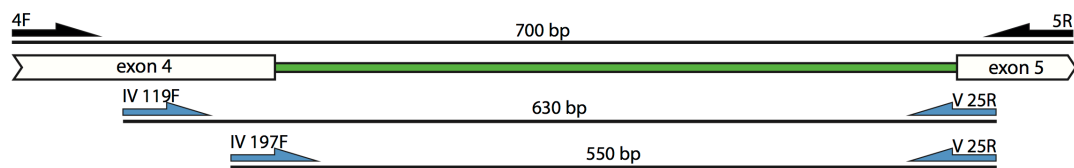
ndhF*rpl32 - trnL**PepC*

Figure 1. Primer map for *ndhF*, *rpl32-trnL* and *PepC* with regions of interest marked in green. Average fragment sizes are indicated between each primer pair, represented by arrows: black (previously published primers), blue (newly developed primers for amplification and sequencing) and yellow (additional sequencing primers developed). The red zigzag patterns represent the position of the homopolymeric regions occasionally found in *rpl32-trnL*.

Capítulo 4

**Molecular phylogeny of *Bignonia* L. (Bignoniaceae)
identifies meaningful morphological units within this
patchworky genus**

A ser submetido para:

Molecular Phylogenetics and Evolution

Phylogeny of *Bignonia* L. (Bignoniaceae, Bignoniaceae)Alexandre R. Zuntini^{1,2} and Lúcia G. Lohmann^{1,2}

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Acknowledgments:

We are grateful to Alice Calvente, Benoit Loeuille, Elaine Françoso and Tatiana Silvana Correa for their assistance with sanger sequencing and Monica Carlsen for her assistance with high throughput sequencing; CEFAP-USP, LGEA-USP and GaTE Lab-USP for logistical support; and Charlotte Taylor for discussions about morphology. We also thank the curators of the MO and SPF herbaria for allowing DNA extraction from specimens. This paper is part of the PhD dissertation of ARZ and was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) as two scholarships to ARZ (2011/09160-5 and 2013/08657-9), a regular research grant to LGL (2011/50859-2), a FAPESP/BIOTA - NSF/DIMENSIONS grant (2012/50260-6), and by CNPq for a Pq-1 grant to LGL (307781/2013-5).

Abstract

Modern classification systems based on phylogenetic information are changing the circumscription of many taxa. The plant family Bignoniaceae, for instance, is known for historically presenting complex generic classification systems and one of the lowest species/genus ratios among the angiosperms. *Bignonia* L., the first genus named in this family, has been circumscribed quite differently in the past, with the number of species included in the genus ranging from 173 species to a single one. As currently circumscribed, the genus embraces 28 species that were placed in 9 different genera in the previous classification system. In its current circumscription, *Bignonia* is highly diverse morphologically, and broadly distributed from Mexico and EUA to Argentina. Here we reconstruct the phylogeny of *Bignonia* using a combination of Sanger and Next Generation Sequencing in order to evaluate the existence of morphologically recognizable clades and the monophyly of currently recognized species. Data derived from the combined sequencing strategy led to a robust phylogenetic tree and allowed the identification of morphological synapomorphies for the genus as whole and for ten different clades that correspond to previously recognized genera. Except from *Bignonia binata*, all other species were shown to be monophyletic.

Introduction

The purpose and types of information used to propose classification systems changed substantially over time. While earlier classification systems pursued “natural” order (e.g. Linnaeus, 1767), based on few labile characters and without a clear definition about the true meaning of natural (Stevens, 1997), modern systems, designed after Hennig (1965), are based on phylogenetic information and focus primarily on the identification of monophyletic taxa that are easily recognizable by morphological synapomorphies (Mayr, 1981). For instance, the Angiosperm Phylogeny Group (APG, 2009, 2003, 1998) reorganizes higher taxonomic ranks of all flowering plants (e.g., families, orders, etc.) by recognizing only monophyletic groups that are recognizable by macro-morphological synapomorphies (APG, 1998). The systematics of large plant families (e.g., Asteraceae, Leguminosae) has followed the same criteria in order to reevaluate infra-familial groupings and infra-generic boundaries.

Another good example of how phylogenetic information can help shaping classification systems is found in Bignoniaceae. This family was known for the smallest average genera size among plant families with more than 400 species, which indicated the urgent need of a generic reclassification (Gentry, 1973a). Most of these small genera were found in the tribe Bignonieae, the largest tribe of the Bignoniaceae (Olmstead et al., 2009), which included 30 genera with up to three species and an average of 7.6 species/genus in the past (compiled from Gentry, 1973a). Bignonieae is clearly monophyletic (Olmstead et al. 2009) and mostly includes lianas with terminal leaflets modified into tendrils and a special pattern of cambium activity that leads to the formation of four to multiple phloem wedges (Lohmann, 2006). As currently circumscribed, Bignonieae includes 393 species and 21 genera, an average of 18.7 species/genus, all of which are supported by morphological synapomorphies (Lohmann and Taylor, 2014). While some genera of Bignonieae have had stable circumscriptions in the past (e.g., *Anemopaegma*, *Lundia* and *Pleonotoma*), the circumscription of others (e.g., *Adenocalymma*, *Amphilophium*, *Dolichandra*, *Fridericia* and *Tanaecium*) have varied considerably overtime and were deeply changed and designated as emendavit (Lohmann and Taylor, 2014). The diagnosis of *Bignonia* was also changed considerably by Lohmann and Taylor (2014). However, given that the characterization of this genus varied so extensively over time, there is no stable reference circumscription against which to measure the change in its

classification and the genus was not formally designated as emended in that treatment.

Bignonia was monotypic in the past, including only *Bignonia capreolata* L. from southern USA and is currently circumscribed more broadly as to accommodate the 28 species that were included in *Cydista*, *Clytostoma*, *Macranthisiphon*, *Mussatia*, *Phryganocydia*, *Potamogonos*, *Roentgenia* and *Saritaea* in the past. In its current circumscription *Bignonia* is characterized by cylindrical or tetragonal stems with eight phloem wedges, 2-foliolated leaves with dense glandular fields in the vein axils of the leaflets, simple or lepidote trichomes, simple or sometimes shortly 3-parted tendrils, prophylls of the axillary buds that are foliaceous, “bromeliad-like” or both, a single series of ovules on each placenta, reticulate pollen exine, and opaque seed wings (Lohmann and Taylor, 2014). As discussed by Lohmann & Taylor (2014: 416), the morphological affinities between *Clytostoma*, *Cydista*, *Mussatia*, *Phryganocydia*, *Potamogonos* and *Roentgenia* were previously hypothesized based on floral traits (Gentry, 1974a; Hauk, 2002, 1997).. More specifically, the nectariferous disk below the ovary is undeveloped and all genera have a dorso-ventrally flattened corolla (except *Mussatia*) and prominent nectar guides. Another predicted similarity was between these six genera and *Saritaea*, due to prophylls and corolla shape (Gentry, 1973b); and between *Macranthisiphon* and *Saritaea*, based on pollen morphology (Gentry and Tomb, 1979). In this sense, the only unpredicted kinship was *Tanaecium nocturnum* (Barb.Rodr.) Bureau & K. Schum. and *B. capreolata*.

Bignonia is well-supported as monophyletic however, the phylogenetic framework that is currently available for Bignoniaceae only aimed at testing generic monophyly and reconstructing relationships among genera (Lohmann, 2006). As a result, the 13 (out of 28) species sampled were insufficient to clearly resolve relationships within the genus (Lohmann, 2006). A broader sampling, including a higher number of taxa and markers, as well as a higher number of individuals per species is greatly needed in order to fully resolve internal relationships in this morphologically diverse and broadly distributed genus that occurs throughout the Neotropical region (Lohmann et al., 2013).

Here we reconstruct the phylogeny of *Bignonia* using Sanger and high throughput sequencing to further test the monophyly of genus and currently circumscribed taxa, evaluate patterns of morphological variation in the group and potentially meaningful morphological sub-units.

Materials and Methods

Taxon sampling

We sampled 76 accessions, representing all species of *Bignonia* (Appendix A), except *B. neouliginosa* for which we were unable to obtain DNA sequences. Multiple accessions were generated for most species sampled species, except from *B. costata*, *B. hyacinthina*, *B. magnifica*, *B. neoheterophylla*, *B. phellosperma* and *B. pterocalyx*, for which a single individual was sampled. Eleven outgroups from *Amphilophium*, *Anemopaegma*, *Mansoa* and *Pyrostegia* were selected based on Lohmann (2006). 69 previously generated sequences (Lohmann, 2006; Zuntini et al., 2013) were combined with 311 sequences that were newly generated for this study.

DNA extraction

Total DNA was extracted using the Invisorb Plant Mini Kit (Invitex, Berlin, Germany) and following the manufacturer's protocol. For herbarium materials, the final elution step was modified from 200 μ l to 50 μ l, as suggested by Zuntini et al. (2013). For one recalcitrant sample (*B. costata*), total DNA was purified using Agencourt AMPure XP Beads (Beckman Coulter, Pembroke Pines, USA), following the manufacturer's protocol for purification of PCR products, with an additional 70% ethanol wash step.

Sanger sequencing

Two chloroplast markers, *ndhF* and *rpl32*, and one nuclear marker *pepC*, were selected for the present study after considering a variety of other molecular markers that had been tested in previous studies (Kaehler et al., 2012; Lohmann, 2003; Zuntini, unpubl. data). The amplification of the chloroplast markers followed Zuntini et al. (2013), and the products were then purified using Illustra ExoStar (GE, Buckinghamshire, UK) and sequenced in Macrogen (Seoul, Korea). Amplification of the nuclear marker (*pepC*) was purified with an Illustra GFX™ Purification kit (GE, Buckinghamshire, UK) following the manufacturer's protocol. Some samples yielded low amounts of amplified DNA and the products of multiple PCR reactions were pooled prior to the purification. In those cases, samples were eluted in 50 μ l of ddH₂O instead of using the supplied buffer. These samples were dried on a vacuum centrifuge (Eppendorf Concentrator 5301) and resuspended in 7 μ l of ddH₂O. The purified products, from regular or concentrating protocols, were inserted into a

pGEM® Easy Vector (Promega, Maddison, USA) and transformed into heat-shock competent cells (JM109, Promega, Maddison, USA). Transformant colonies were resuspended in 10 µl of ddH₂O. PCR products derived from each of these resuspended colonies were purified using Illustra ExoStar and sequenced in MacroGen (Seoul, Korea). See Zuntini et al. (2013) for further details on the PCR protocols.

Sequences were edited and analyzed in Geneious 7.1 (Biomatters) and aligned using Muscle (Edgar, 2004) under standard parameters. In the rpl32-trnL matrix, a four bp inversion site [positions: 400–404] was visually identified and this micro-inversion was removed from the final dataset.

High-throughput sequencing

Eight species of *Bignonia* (*B. aequinoctialis*, *B. bracteomana*, *B. capreolata*, *B. corymbosa*, *B. magnifica*, *B. nocturna*, *B. potosina* and *B. uleana*) and one outgroup (*Mansoa standleyi*) were sequenced using an Illumina Plataform. Total DNA was quantified using Nanodrop and diluted with ddH₂O to a final volume of 50µl at 100 ng/µl. Diluted samples were transferred to microAFA-tubes and sonicated using Covaris S-series (at CEFAP-USP), with the following parameters: 175W of incident power, 10% duty factor, 200 cycles and 50s. The fragmented samples (mostly 200 – 300 bp) were used to prepare libraries using NEBNext DNA Library Prep Master Mix and NEBNext Multiplex oligos (New England Biolabs, Ipswich, USA), following the manufacturer's protocol with modifications proposed by M. Carlsen (Pers. comm.). Libraries were quantified via qPCR on an ABI7300 RT-PCR, using a KAPA Library Quantification Kit for Illumina Sequencing Platforms (Kapa Biosystems, Wilmington, USA). Samples were diluted in ddH₂O to a final concentration of 2nM and 10µl and diluted libraries were pooled together. The final pool was sequenced, in a pair-end mode, on an Illumina HiScanSQ at the Laboratório Multiusuários Centralizado (ESALQ-USP, Piracicaba, Brazil).

Demultiplexed reads were cleaned using Seqclean (<https://bitbucket.org/izhbannikov/seqclean>), discarding bases with quality scores below 20 and shuffling paired reads. The reconstruction of plastomes involved the analyses of cleaned pair-ended reads using two approaches: (1) Reference mapping using *Olea europaea* (NC_013707). Mapping was conducted in Geneious 7.1, with five iterations and using a 80% identity threshold. The final contig was inspected and

alignment disagreements were manually corrected; (2) De novo assembling using Velvet (Zerbino and Birney, 2008). In this analysis, pair-ended reads and kmer size were fixed at 65 after an evaluation of alternative values. The expected insert length was set to 200bp and a cut-off coverage was defined as half of the average coverage of coding regions from single-copy portions obtained from the reference mapping analysis, in order to eliminate the assemblage of mitochondrial scaffolds.

Contigs obtained from reference mapping and *de novo* assembly were aligned in Geneious, where final scaffolds were produced. The fragments of plastomes for each species were aligned with progressive MAUVE (Darling et al., 2010) implemented in Geneious. Regions not assembled for all species were discarded. Fragments were annotated using DOGMA (Wyman et al., 2004) and the “Live annotation” plugin in Geneious, using the *Olea* plastome as reference; annotations from each method were compared.

Phylogenetic analyses

The three molecular matrices produced through Sanger sequencing (ndhF, rpl32-trnL and pepC) were analyzed separately, under parsimony (MP) and Bayesian (BI) criteria. For pepC, two separate matrices were prepared: the first included all clones sequenced while the second included a single randomly selected clone per accession. Clones from the second matrix were combined with the ndhF and rpl32-trnL data matrices to produce a combined molecular matrix. Another matrix (cpDNA), containing only the chloroplast markers was also prepared.

Parsimony analyses were performed in PAUP 4.0b10 (Swofford, 2003) with 100 initial searches for the shortest tree. Initial trees were subject to further swapping and the resulting trees were summarized in a strict consensus tree. Clade support was estimated using 1000 bootstraps replicates. For the Bayesian inference, substitution models were selected by jModelTest 2.1.4 for each data partition (Darriba et al., 2012; Guindon and Gascuel, 2003). The DNA substitution model TVM+G was selected as the best fit model for the cpDNA data partition (ndhF and rpl32-trnL) and the TPM1uf+G substitution model was selected as the best data partition for the nDNA dataset (pepC). Analyses were conducted in MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) using two simultaneous runs, each with 10 million generations and 4 chains, and sampling one tree every 1000 generations. Once stationarity was confirmed, the first 25% of sampled trees was discarded and the remaining trees were used to

compute a majority-rule consensus tree and to assess posterior probabilities of clades. Clade support of clades is indicated as “(bootstrap/posterior probability)” throughout the text. Clades with support lower than 50% or not recovered in any analyses are represented by hyphens.

To reconstruct the backbone of the *Bignonia* phylogeny, we used the same methodology and parameters described above, except from a reduction to 2 million generations in the Bayesian inference. The genomic matrix was analyzed under six different partition schemes: (1) whole alignment without partitioning; (2) individual genes and spacers; (3) only spacers; (4) only coding regions, unpartitioned; (5) only coding regions, partitioned by codon position; and (6) same as (5), but using only the 1st and 2nd bases of each codon. For each partition in each scheme, the best-fit model was selected in jModelTest 2.1.4.

The final molecular dataset (ndhF, rpl32-trnL and pepC) with 76 terminals was then re-analyzed setting the backbone topology obtained as a topological constraint. A subset of the comprehensive matrix, containing only one accession per species (41 terminals) was also re-analyzed using the same topological constraint.

Morphological analyses

A dataset with 43 morphological characters compiled for the taxonomic revision of *Bignonia* (Zuntini, Taylor and Lohmann, in prep.) was used in ancestral character state reconstructions. This dataset included only categorical data, coded as either binary or multistate (Appendix B). The morphology of outgroups was coded based on available taxonomic treatments (Gentry, 2009; Pool, 2009, 2008, 2007; Silva-Castro, 2010) and complemented by the analysis of selected specimens. Pollen data was compiled from Gentry and Tomb (1979). Ancestral character state reconstructions were conducted in Macclade 4 (Maddison and Maddison, 2003), using parsimony assumptions; no optimization criteria was implemented.

Results

Sanger sequencing

Complete sequences were obtained for almost all terminals (Appendix A). The ndhF matrix contained 74 terminals and 2094 characters (392 variable/288 parsimony informative) while the rpl32-trnL included 68 terminals and 1158 characters (264/159), and the pepC dataset included 72 terminals and 613 characters (329/216).

The simplified DNA matrix, with a single accession per species included 41 taxa and 3814 characters, of which 909 were variable and 393 were parsimony informative.

High-throughput sequencing

The number of raw paired-reads varied from 6.7 to 13.1 million reads (Table 1). For most species, the average coverage of single copy coding regions was over 250x, except for *B. bracteomana* and *B. potosina*, which presented an average coverage that was lower than 50x. This small coverage was comparable to the mitochondrial genome coverage, preventing us from reassembling the portions of the plastome that presented high similarity with the mitochondrial genome (e.g., the cpDNA genes *atpF*, *atpI*, *rpoB*, *rpoC1* and *rpoC2*).

Duplicated regions (IRa) and portions unavailable for all accessions were removed and contigs were aligned. Portions that were not confidently aligned were discarded. After all the data cleaning, the “whole alignment” partition presented 80,946 characters, with 3,688 (4.5%) variable characters and 572 (0.7%) that were parsimony informative. Spacers and coding region (CDS) partitions presented 25,906 and 39,177 characters respectively, with 5.5% and 4.3% variable sites. Despite the low variation of the CDS partitions, these regions presented more parsimony informative sites: 337 (0.8%) against 168 (0.6%) sites (Table 2).

Phylogenetic reconstruction

Analysis of the ndhF, rpl32-trnL and pepC data matrices. The analyses of the individual data matrices showed different levels of resolution. In general, cpDNA data (*ndhF* and *rpl32-trnL*) recovered relationship among main lineages of *Bignonia* and outgroups, while the nDNA (*pepC*) data refined relationship among closely related species. For each matrix, parsimony and Bayesian criteria recovered similar topologies, the latter with less polytomies and higher clade support. Although relationships among lineages were congruent between plastid (cpDNA) and nuclear (*pepC*) partitions, the internal topologies within clades differed between markers. Differences were generally insignificant and usually not recovered in the MP analyses and with low posterior probability (<50%) in the BI (Fig. 1).

The most significant incongruence is observed in the clade that is sister to *B. campanulata* (dashed arrow in Figure 1). In the topology derived from the analysis of the *pepC* dataset, six clades were retrieved: (1) *B. uleana* and *B. aff. uleana*, sister to

(2) Two accessions of *B. sciuripabula* and one of *B. callistegioides*. Sister to this clade, we observe a tritomy between (3) Two other accessions of *B. sciuripabula* and one accession of *B. callistegioides*, (4) *B. aff. binata*, *B. cuneata* and *B. pterocalyx* and a clade formed by a second accession of *B. aff. binata*, (5) *B. binata* and (6) *B. convolvuloides* and *B. ramentacea*. On the other hand, in the topology derived from the analysis of the cpDNA dataset, all accession of *B. binata*, *B. callistegioides* and *B. sciuripabulum* (clades 2, 3 and 5) form a clade that is sister to clade 6, which is, in turn, sister to the clade formed by clades 1 and 4. Another topological incongruence observed is associated with the placement of the sample identified as *B. aff. hyacinthina*. In the topology derived from the analysis of the cpDNA dataset, this sample emerges in a polytomy with all accessions of *B. prieurii* (96%/100%) whereas this sample appears as sister of *B. hyacinthina* (-/99%) in the topology derived from the analysis of the pepC dataset.

Analysis of the combined molecular dataset (ndhF+rpl32-trnL+pepC).

Despite the incongruences encountered, the two matrices were combined leading to higher resolution and support. In the combined molecular analyses, the genus is reconstructed as monophyletic (100%/100%) with eight highly supported clades: (1) *B. magnifica* and *B. longiflora*; (2) *B. capreolata*; (3) *B. nocturna*; (4) *B. bracteomana* and *B. sordida*; (5) *B. aequinoctialis*; (6) *B. costata*, *B. decora*, *B. diversifolia*, *B. lilacina* and *B. potosina*; (7) *B. corymbosa*, *B. hyacinthina*, *B. aff. hyacinthina*, *B. microcalyx*, *B. neoheterophylla*, *B. phellosperma* and *B. prieurii*; and (8) *B. binata*, *B. aff. binata*, *B. callistegioides*, *B. campanulata*, *B. convolvuloides*, *B. cuneata*, *B. pterocalyx*, *B. ramentacea*, *B. sciuripabulum*, *B. uleana* and *B. aff. uleana* (Suppl. 1-A). Overall, relationships among species within each clade are well resolved. In addition, affinities among lineages 1 and 2 are well resolved, while the affinities among lineages 3 to 7 are poorly resolved.

The backbone reconstructed from the analysis of each data partition was somewhat divergent, although several of these relationships were only poorly supported in each analysis. Main divergences were associated with: (i) the placement of clade D, which was resolved either as sister to E (partition schemes 1, 3, 4, 5 and 6) or as sister to clade J (scheme 2); and (ii) the placement of clade B, which was resolved as sister to C or as the basalmost lineage of the genus. Since all partitions produced trees with similar indexes (Table 2), the topology obtained from partition 6 (first and second bases of CDS) is the most conservative given that the first two bases

of each codon tend to accumulate less homoplasy (Källersjö et al., 1999). The same topology was also obtained for the schemes 1, 4 and 5.

Analysis of the combined molecular data matrix and genomic dataset. The final topology obtained from the analysis of the combined molecular matrix constrained by the backbone obtained through the analysis of the genomic dataset led to a fully resolved topology until the species level; only relationship among accessions of *B. binata* and within the *B. convolvuloides*/*B. ramentacea* species complex were not fully resolved.

In the resulting topology, *B. nocturna* is strongly supported as the first diverging species (100%/100%) in the genus. A monophyletic *B. capreolata* is the second diverging lineage in the genus, followed by a clade composed of *B. magnifica* and *B. longiflora* (100%/100%). The following lineage to diverge is a clade composed of *B. bracteomana* and *B. sordida* (100%/100%), which is sister to the core *Bignonia*. The core *Bignonia* clade includes three major sub-clades, one that includes previous members of *Cydista* (clade F), which is sister to a clade that includes two sub-clades: one composed of previous members of *Clytostoma* (clade J), and the other (GHI) including members of *Potamogonos* and *B. neoheterophylla* (clade H), as well as members of the previously recognized *Mussatia* (clade J) and *Phryganocydia* (clade I). The relationship within each of clades F through J are described below:

Clade F – In this clade, the first species to diverge is *B. aequinoctialis* (100%/100%), followed by *B. diversifolia* (98%/100%), then *B. potosina* (98%/100%), and finally *B. decora* (63%/86%) which is sister to *B. costata* and *B. lilacina* (89%/100%).

Clade GHI – Here, the clade G (75%/95%) is sister to H and I (98%/100%), and includes *B. microcalyx* and *B. neoheterophylla*. The clade H (100%/100%) is composed by *B. corymbosa* and *B. phellosperma* and is sister to clade I (100%/100%), which includes *B. hyacinthina*, *B. aff. hyacinthina* and *B. prieurii*.

Clade J – The first species to diverge is *B. campanulata*; sister to it, two lineages are retrieved (100%/100%). In the first (-/94%), *B. uleana* and *B. aff. uleana* (100%/100%) are sisters to the clade formed by *B. aff. binata*, *B. cuneata* and *B. pterocalyx*. In this clade (96%/100%), one accession of *B. aff. binata* is first to diverge, followed by *B. pterocalyx*, sister to the second accession of *B. aff. binata* and *B. cuneata*. The second lineage (79%/100%) of clade J is composed by *B. binata*, *B. callistegioides*, *B. convolvuloides*, *B. ramentacea* and *B. sciuripabulum*. One clade

(94%/100%) formed by one accession of *B. callistegioides* and two of *B. sciuripabulum* is the first to diverge. Sister to this, a clade with the three accession of these last two species is found (52%/99%) and is sister to it, a clade with *B. binata* (82%/100%) sister to polytomic (89%/100%) *B. convolvuloides* and *B. ramentacea* (Fig. 2).

This topology was almost identical to the topology obtained from the single accession subset. From this matrix, containing 41 taxa and also constrained by the backbone, a completely resolved phylogeny was obtained. All clades presented maximum support (from BI) except four, of which three had posterior probability above 90% (Fig. 3). The only weakly supported clade (-/70%) is formed by *B. decora* and *B. potosina*, sister to *B. costata* and *B. lilacina*, and is the only incongruence with the comprehensive where *B. potosina* it the first diverging lineage.

Morphological analyses

The topology that included a single accession per species was used as basis for ancestral character state reconstructions. This analysis allowed the identification of morphological synapomorphies for 11 strongly supported clades (Table 3, Fig. 3). Some of the synapomorphies identified are non-homoplastic like the undeveloped nectariferous disk (clade C), the sessile lateral inflorescences (clade D), the spatheous calyx (clade H) and the verrucose ovary (clade J). Other synapomorphies are homoplastic but still quite useful for the recognition of selected clades. For instance, leaf domatia and verrucose fruit surface are both homoplastic synapomorphies for clades D and I, whereas axillary inflorescence emerge as synapomorphy of clade G and the clade composed of *B. aff. binata* + *B. cuneata*. Synchronous flowering and flattened corolla are synapomorphies of clade C with a posterior reversion in *B. campanulata*, while the opaque seed wings is an additional synapomorphy of clade C followed by three independent reversions.

Discussion

Here we present a comprehensive phylogeny of *Bignonia* which was reconstructed using traditional Sanger sequencing and high-throughput sequencing. With this combined methodology, it was possible to obtain a well resolved and supported phylogeny for the genus. This phylogenetic framework provided further support for the monophyly of *Bignonia* and for the inclusion of the monotypic and

morphologically distinctive genus *Macranthisiphon* into the genus. *Macranthisiphon longiflorus* was included in *Bignonia* solely based on morphological characters (Lohmann and Taylor, 2014) and the molecular evidence gathered here further supported this taxonomic decision. *Bignonia neouliginosa*, the only species for which we were unable to obtain DNA sequences could be temporarily placed within clade H due to its morphological similarity with *B. corymbosa* and by sharing both morphological synapomorphies of this clade (Tab. 3). The future addition of this taxon to the molecular will test this hypothesis.

Backbone phylogeny

The addition of high-throughput sequencing aimed at resolving the polytomy associated with the five key lineages of clade C, which is presumed to have resulted from rapid radiation given the very short branch lengths (Fig. 2). This rapid radiation seems to have been followed by the accumulation of many mutations in each terminal given the long terminal branches recovered (Fig. 2-A). These mutations are much more abundant in spacer or intronic regions than in coding regions, but apparently did not increase the amount of molecular homoplasy (Tab. 2). In addition, many micro-inversions of 2–10 bp in length, were observed. These micro-inversions are often located between complementary sequences, which form secondary structures (hairpins) that facilitate the occasional switch of the apical portion, randomly creating inversions (Kelchner and Wendel, 1996). Such inversions tend to induce equivocal topologies due to the overweight of single mutation events (Kim and Lee, 2005) and should thus, be excluded from phylogenetic analyses. Cumulative homoplasies and micro-inversions are more common in non-coding regions, which may have lowered the accuracy of the backbone reconstruction based on partition schemes that included spacer regions, leading to unlikely phylogenetic scenarios.

Coding regions are less variable when compared to genic spacers, which would counteract the effect of long branches. Although the usage of these regions would be counter-intuitive to refine rapid radiation polytomies, we found more informative sites when compared to spacer regions (Tab. 2), which produced a robust backbone that is consistent with our morphological data. For instance, clade A (all *Bignonia* except *B. nocturna*) has two synapomorphies (stipitate prophylls and flattened fruits) while clade E, sister to *B. bracteomana* and *B. sordida*, also has two synapomorphies: bromeliad-like prophylls and compound lateral dichasia (Fig. 3). On the other hand,

rival backbone topologies, like the closer affinity between clades D and J, reconstructed from spacer partition would invalidate the two synapomorphies of the clade E mentioned above and also the echinate fruit, a remarkable synapomorphy of clade J.

Morphological synapomorphies of Bignonia

The current circumscription of the genus was proposed based on a series of morphological affinities between the taxa included in this clade. In particular, the cylindrical and tetragonal stems with eight phloem wedges, 2-foliolated leaves with dense glandular fields in the vein axils of the leaflets, simple and lepidote trichomes, simple and sometimes shortly 3-parted tendrils, a single series of ovules on each placenta, reticulate pollen exine (Lohmann and Taylor, 2014). In addition, Lohmann and Taylor (2014) indicated that prophylls of the axillary buds that are foliaceous, “bromeliad-like” or both, and opaque seed wings might represent morphological synapomorphies for the genus. However, our extended sampling allowed us to identify the opaque seed wings as a synapomorphy of clade C instead. The coding of the prophyll character was refined here and divided into several characters (5 to 9, Appendix B). In particular, coding the first pair of prophylls (foliaceous part) from the consecutive pairs (bromeliad-like form) seemed to be a better coding strategy given the principle of positional homology (Remane, 1952). With this refinement, the bromeliad-like prophylls arose as a putative synapomorphy of clade E, whereas the foliaceous prophylls are apparently simplesiomorphic. The simple tendril was reconstructed as the only putative synapomorphy of *Bignonia*, but it is homoplastic due to existence of multifid tendril in *B. capreolata*. The same result was also observed by Sousa-Baena et al (2014).

Meaningful morphological groups

Most of the strongly supported clades of *Bignonia* can be recognized by putative synapomorphies. Not surprisingly, many of these clades represent previously accepted genera such as *Clytostoma*, *Cydista*, *Mussatia* and *Phryganocydia*, while their synapomorphies, respectively, echinate fruits, quadrangular stems, bilabiate corolla and spathaceous calyx were diagnostic characters of each genus. The monophyly of the dytypic *Mussatia* and *Phryganocydia* was here confirmed. In addition, several taxa previously included in *Clytostoma* and *Cydista* were also shown

to be monophyletic (Fig. 3). More specifically, all species from previously included in *Clytostoma* (clade J) formed a clade, except from *B. costata* which fell within clade F, which includes most species of the previously recognized *Cydista*., which is further characterized by more than two series of ovules per locule, stems without lateral projections, and falcate, caducous prophylls. Four of the five species previously recognized in *Cydista* form a clade (clade F) together with *B. costata* (previously *Clytostoma*). The fifth species of the previously recognized *Cydista* (*B. neoheterophylla*) appears as sister to *B. microcalyx* (clade G), which was previously included in *Potamogonos*. Even though *B. neoheterophylla* differs by the absence of interpetiolar gland-fields and apically trifid tendrils, it shares minute prophylls and axillary racemes with *B. microcalyx*.

Despite the fact that several of the genera recognized under earlier classification systems and included in clade C are monophyletic in most part, species included in clade C share oblong or elliptic fruits and opaque seed wings (Tab. 3). In addition, members of clade C also share a reduced nectariferous disk, synchronous flowering (except *B. campanulata*) and dorso-ventrally flattened corollas, all of which are associated with a mimetic pollination system in which flowers would attract pollinators without offering nectar as resource, assuring cross pollination and saving energy (Gentry, 1974b). The development of this floral morphology might represent a key innovation of clade C, which may have contributed to the rapid radiation observed in this clade. Even though the clade is much more diverse than its sister clade (24 vs. 2 spp.), this difference in species number is not enough to validate a key innovation hypothesis (Hunter, 1998), and the role of this pollination system remains to be properly tested.

The previously hypothesized close affinities between *B. longiflora* and *B. magnifica* due to the unique pollen morphology: polyporate pollen grains, with a complex exine pattern, formed by edges radially disposed around the pores (Gentry and Tomb, 1979), were also corroborated in the present study. Despite the pollen morphology, the tubular calyx is also a putative synapomorphy of this clade (Tab. 3).

Species circumscription

Most species emerged as monophyletic in all data partitions, corroborating the circumscription of some widespread taxa like *B. aequinoctialis*, *B. corymbosa* and *B. prieurii*. For these taxa, although internal resolution is observed, there are no

morphological breaks that justify fragmentation, even at infraspecific levels and the recognition of varieties is not supported (Gentry, 1973a; Hauk, 1997).

The only widespread species that is clearly paraphyletic is *B. binata*, within which two independent lineages can be recognized (Fig. 1–2). The first lineage is the one that is morphologically most similar to the type of *B. binata*. This lineage emerges within a polytomy with *B. callistegioides* and *B. sciuripabulum* in the cpDNA tree, and in a clade that includes *B. convolvuloides* and *B. ramentacea* in the pepC and concatenated trees. It is distributed from Northeastern Brazil to Argentina and Paraguay, overlapping with its related species and occurring in various habitats within the Atlantic forest. The second lineage identified as *B. aff. binata*, appears as closely related to *B. cuneata* and *B. pterocalyx* in all partitions. Members of this lineage are distributed from Mexico to Bolivia and Brazilian Amazonia, where it occurs in close association with water bodies such as the flooded forests. This second lineage has corky and wingless seeds, any may be adapted to hydrochory. On the other hand, the “typic” lineage has winged and slender seeds and might be adapted to wind-dispersal. These two forms have long treated as a single species (Bureau and Schumann, 1896; Lohmann and Taylor, 2014; Sandwith, 1937), despite the morphological and ecological differences. The phylogenetic data here presented further supports a re-circumscription of *B. binata* (Zuntini, Taylor & Lohmann, in prep.).

The relationship between *B. binata* and its closely related species differs in the cpDNA and nDNA trees. While the nuclear marker places it more closely related to *B. convolvuloides* and *B. ramentacea*, the plastid markers recover an unresolved clade with *B. binata*, *B. callistegioides* and *B. sciuripabulum*. These three species are morphologically similar and are commonly misidentified. The fact that these species present the mimetic system, overlapping distribution patterns and flowering periods may facilitate natural hybridization, which would explain the variability between these species and morphological overlap between them.

The clade composed of *B. convolvuloides* and *B. ramentacea* is sister to *B. binata* in the nuclear and combined datasets. This relationship was strongly supported in all analyses, but with little internal resolution. Both species present similar indument and congruent distribution patterns, ranging from the Brazilian scrublands (caatinga) and savannas (cerrado), through the Chaco (Bolivia and Paraguay). These species are distinguished exclusively by the developmental stage of leaves during

flowering, with *B. convolvuloides* showing mature leaves while *B. ramentacea* is mostly leafless or bears very young leaves during blossoming (Bureau and Schumann, 1896). These two forms represent extremes of the morphological range and are best treated as a single species (Zuntini, Taylor & Lohmann, in prep.).

The only other clade of *Bignonia* that showed problems associated with species delimitation is clade I. Within this clade, the accession identified as *B. aff. hyacinthina* emerges as sister to *B. prieurii* in the chloroplast and combined molecular analyses and as sister to *B. hyacinthina* in the tree that resulted from the analysis of the pepC dataset. This specimen was collected in Peru, which constituted the distribution limit of both accepted species and where intermediate forms between these two taxa are found. This data might suggest the existence of a hybrid zone between *B. prieurii* and *B. hyacinthina* or may already indicate the existence of a new hybrid species. A detailed phylogeographical study would be needed in order to test this hypothesis.

Conclusions

In this study we reconstructed a robust and comprehensive phylogeny of *Bignonia*, by combining Sanger with high throughput sequencing technologies. The phylogenetic framework of *Bignonia* provided further support for the monophyly of the genus and new insights into the patterns of morphological variation in the genus, allowing the identification of new morphological synapomorphies for ten infra-generic clades. This phylogenetic framework provides the basis for biogeographical and evolutionary studies in the genus, which will provide novel insights into the factors that have shaped such high morphological diversity in the genus (Zuntini & Lohmann, in prep.).

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Table 1. Results from high-throughput sequencing and genomic assemble. Voucher available on Appendix A.

Species	Raw reads (Millions of pairs)	Clean reads (Millions of pairs)	Mean read length (bp)	Number of scaffolds	Total length* (bp)	Average coverage of CDS regions**	GenBank accessions
<i>B. aequinoctialis</i>	11.045	9.230	93	5	128,914	561	XX9999
<i>B. bracteomana</i>	9.234	7.025	89	3	127,666	49	XX9999
<i>B. capreolata</i>	6.746	5.271	91	11	129,429	540	XX9999
<i>B. corymbosa</i>	7.686	5.324	92	5	127,998	305	XX9999
<i>B. magnifica</i>	6.925	5.238	94	1	127,821	1,351	XX9999
<i>B. nocturna</i>	7.940	6.615	91	3	130,962	921	XX9999
<i>B. potosina</i>	7.208	5.732	92	3	128,392	31	XX9999
<i>B. uleana</i>	11.866	9.752	91	5	123,825	456	XX9999
<i>M. standleyi</i>	13.190	11.067	90	3	143,038	257	XX9999

Table 2. Backbone results. PIC = parsimony informative character (bp) = base pairs

Partition scheme	Alignment length (bp)	Variable characters		PIC		Homoplasy index
		Absolute (bp)	Relative (%)	Absolute (bp)	Relative (%)	
Whole alignment	80,946	3,668	4.53	572	0.7	0.3754
Genes and spacers	80,946	3,668	4.53	572	0.7	0.3754
Only spacers	25,906	1,433	5.53	168	0.64	0.3844
Only CDS	39,177	1,711	4.36	337	0.86	0.3716
Only CDS (1+2+3)	39,177	1,711	4.36	337	0.86	0.3716
Only CDS (1+2)	26,118	989	3.78	232	0.88	0.3788

Table 3. Putative morphological synapomorphies of selected clades and their previous taxonomic designation. Names between quotes indicate groups that would be considered paraphyletic under this phylogenetic framework.

Clade	Previous Designation	Putative synapomorphies
<i>Bignonia</i>	-	Simple tendril
A	-	Stipitate prophylls, flattened fruit
B	-	Polyporate pollen, with complex exine patterns; tubular calyx
C	-	Synchronous flowering, undeveloped nectariferous disk, oblong or elliptic fruit, opaque seed wings
D	<i>Roentgenia</i>	Leaf domatia, tendril apically bi-trifid, sessile lateral dichasium, verrucose fruit
E	-	Bromeliad prophylls, compound lateral dichasia
F	" <i>Cydista</i> "	Quadrangular stems
G	-	Minute prophylls, racemes, axillary inflorescences
H	<i>Phryganocydia</i>	Spathaceous calyx
I	<i>Mussatia</i>	Leaf domatia, Opposite percurrent tertiary venation, calyx without glands, bilabiate corolla, oblong or elliptic fruit, verrucose fruit
J	" <i>Clytostoma</i> "	Glabrous and verrucose ovary, echinate fruit, one winged seeds

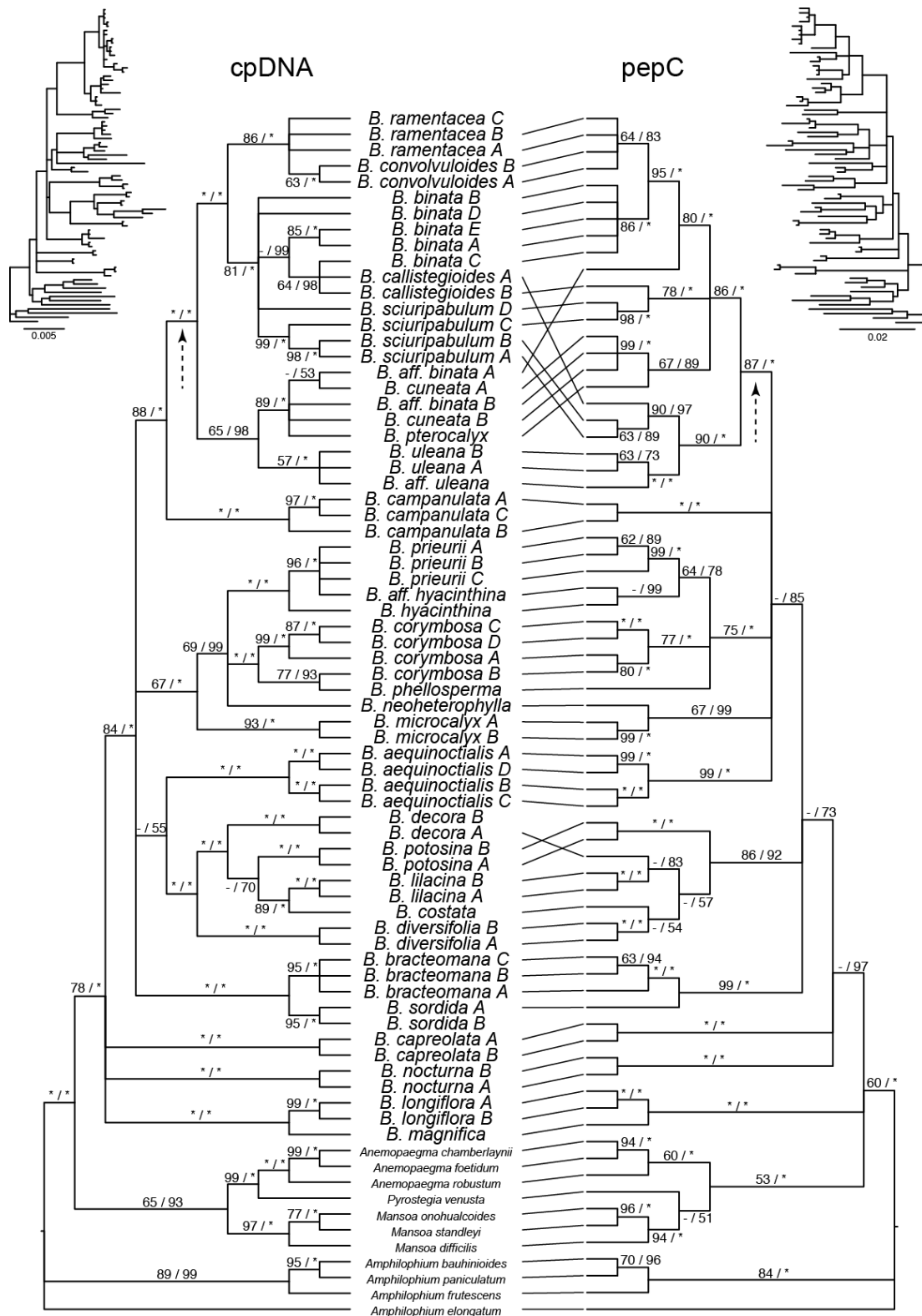


Figure 1. Phylogeny of *Bignonia* with obtained from chloroplast (left) and pepC (right) matrices. Cladogram from Bayesian analyses with respective phylograms at upper corners. Values near branches indicate clade support, in percentage, (Parsimony bootstrap / Bayesian posterior probability). Asterisk indicate 100% and hyphens unretrieved clades.

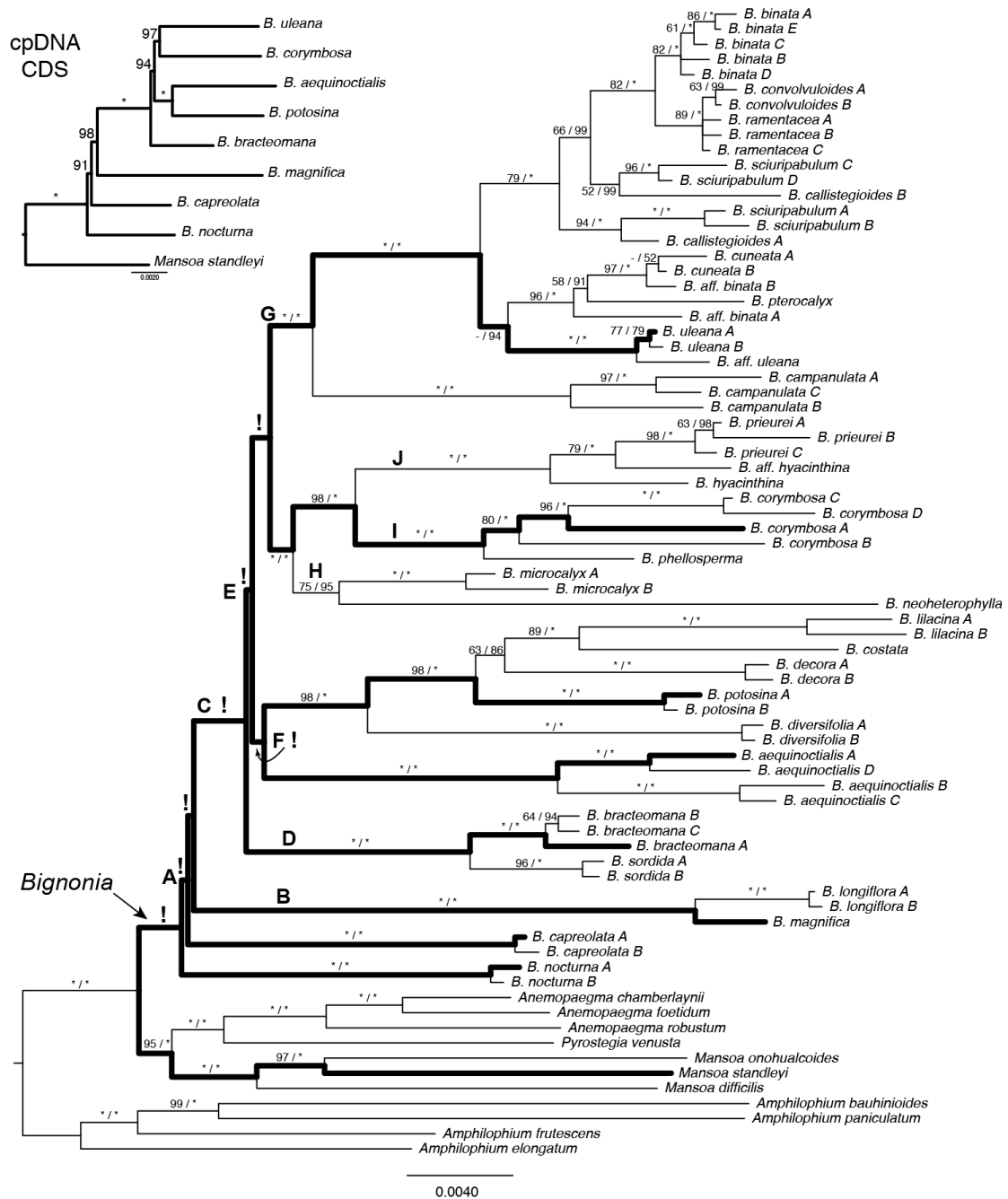


Figure 2. Phylogeny of *Bignonia* (main) and plastomic backbone (upper left). Main: Phylogram from Bayesian analysis and concatenated data. Thicker lines connect specimens sampled in backbone analyses. Values near branches indicate clade support, in percentage, (Parsimony bootstrap / Bayesian posterior probability). Asterisk indicate 100% and hyphens unretrieved clades. Exclamation marks (in bold) specify constrained clades.

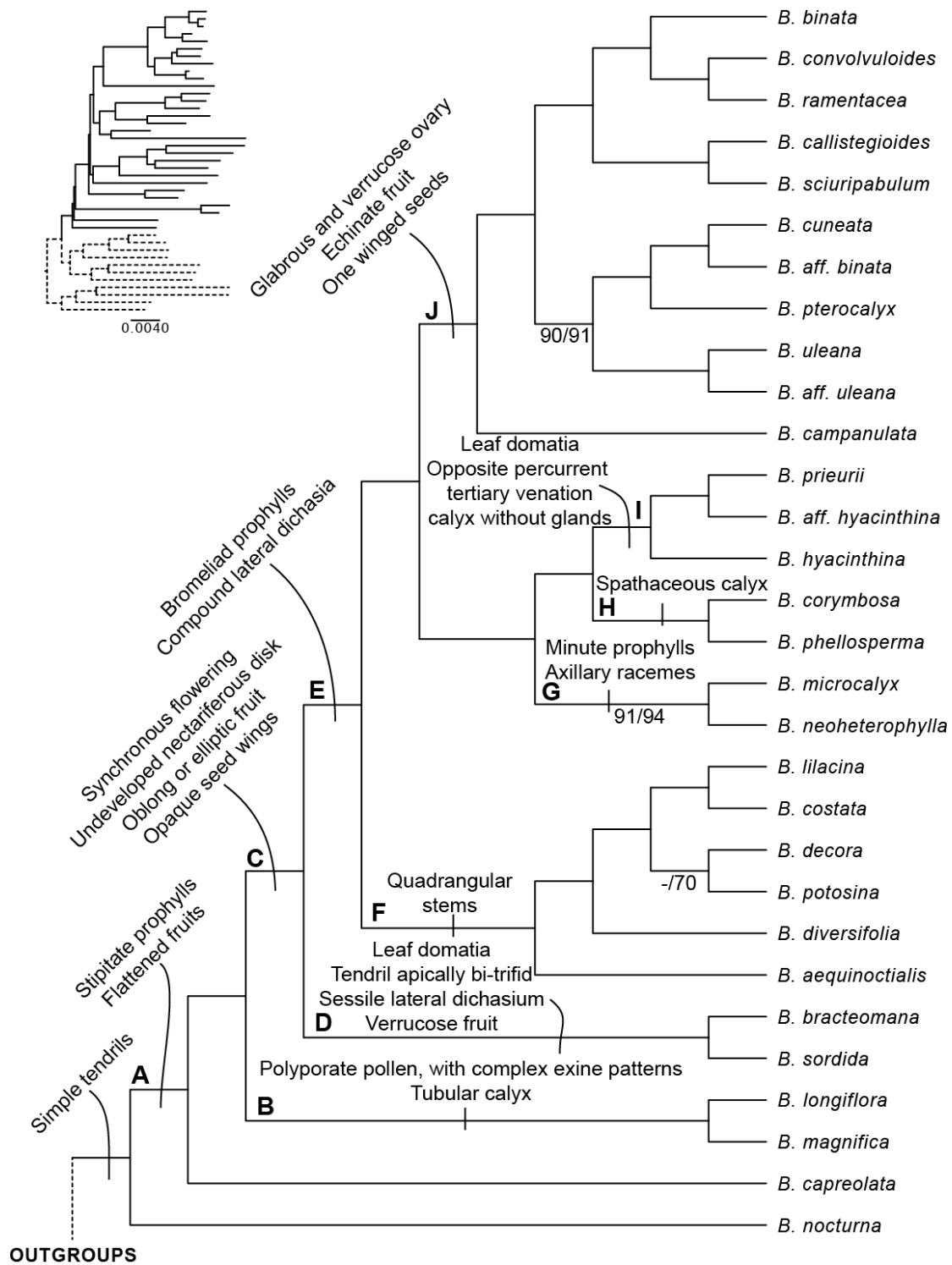


Figure 2. Cladogram of *Bignonia* with synapomorphies (main) and phylogram (upper left). Main: Cladogram obtained from the combined analyses. Values below branches indicate clade support, in percentage, (Parsimony bootstrap / Bayesian posterior probability); absent values indicate maximum support and hyphens unretrieved clades. Synapomorphies according to Table 3. Phylogram from Bayesian analysis: outgroups plotted in dashed lines

Appendix A. Vouchers and Genbank accessions. Species, Locality, *Voucher* (Herbarium), *ndhF*, *rpl32-trnL*, *pepC* clones. Sequences with prefix “XX” were generated in this study. An asterisk near herbarium acronym indicates material extracted from exsiccate, “na” for unavailable sequences and underline voucher indicate samples used in NGS.

Bignonia aequinoctialis L.: “A” – BR, AM, *Nogueira 158* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – BR, AM, *Lohmann 320* (MO): DQ222577, XX9999, DQ222719, XX9999, XX9999; “C” – BR, RR, PN Viruá, *Fonseca* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “D” – BR, AM, Manaus, *Nogueira 160* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. binata*** Thunb.: “A” – BR, SP, PE Vassununga, *Tibiriça sn* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – BR, RJ, Eng. Pedreira, *Matos 1* (RB, SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “C” – BR, PR, Foz do Iguaçu, *Labiak 3837* (SPF, U PCB): XX9999, XX9999, XX9999, XX9999, XX9999; “D” – BR, SP, *Zuntini sn* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “E” – BR, PR, MBM, *Zuntini sn* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. aff. binata*** Thunb.: “A” – BR, AM, *Galvanese 22* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – CR, Guanacaste, PN Palo Verde, *CR 3* (SPF, USJ): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. bracteomana*** (K. Schum.) L. G. Lohmann: “A” – PER, Madre de Dios, Manu, *Lohmann 614* (MO, MOL): DQ222634, XX9999, DQ222806, XX9999, XX9999; “B” – PER, Amazonia, Armango, *Woytkowski 5637* (MO): KC914588, KC914594, KC914610, KC914611, KC914612; “C” – ECU, Napo, *Grijalva 409* (MO, QCNE, SPF): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. callistegioides*** Cham.: “A” – ARG, Misiones, *Fonseca* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – EUA, MO, Saint Louis, *Lohmann 352* (MO): DQ222569, XX9999, DQ222708, XX9999, XX9999; ***B. campanulata*** Cham.: “A” – BR, SP, E.S. Pinhal, *Zuntini 279* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – PER, Madre de Dios, Manu, *Centeno 74* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “C” – BR, MG, Marliétria, *Lombardi 2526* (MO): DQ222570, XX9999, XX9999, XX9999, XX9999; ***B. capreolata*** L.: “A” – EUA, IL, Jonhson County, *Lohmann 356* (MO): DQ222566, XX9999, DQ222706, XX9999, XX9999; “B” – USA, Virginia, Meckleburg, *Reed 53387* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. convolvuloides***

(Bureau & K .Schum.) L.G. Lohmann: “A” – BR, PE, Tupanatinga, *Carvalho 2* (SPF): KC914586, KC914592, KC914605, KC914606, KC914607; “B” – BR, PE, ibimirim, *Gomes 278* (SPF): KC914591, KC914597, KC914617, KC914618, KC914619; ***B. corymbosa*** (Vent.) L. G. Lohmann: “A” – BR, MS, *Pace 111* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – BR, ES, Linhares, *Zuntini 210* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “C” – CR, Puntarenas, OSA, *Zuntini CR 22* (SPF, USJ): XX9999, XX9999, XX9999, XX9999, XX10000; “D” – BR, ES, Linhares, *Lohmann 654* (MO, CVRD): DQ222621, XX9999, DQ222785, XX9999, XX9999; ***B. costata*** (Bureau & K .Schum.) L.G. Lohmann: BR, RJ, Volta Redonda, *Carauta 4933* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. cuneata*** (Dugand) L. G. Lohmann: “A” – VEN, Miranda, *Berry 969* (MO): XX9999, XX9999, XX9999, XX9999; “B” – VEN, Falcón, Silva, *Steyermark 110944* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. decora*** (S. Moore) L. G. Lohmann: “A” – BOL, La Paz, Franz Tamayo, *Loza 470* (MO, SPF): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – BR, MS, Bonito, *Hatschbach 74724* (MBM, SPF): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. diversifolia*** Kunth: “A” – NIC, Chinandega, Cinco Pinos, *Coronado 723* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – CR, Guanacaste, PN Palo Verde, *Zuntini CR 13* (SPF, USJ): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. hyacinthina*** (Standl.) L. G. Lohmann: CR, Heredia, La Selva BE, *Zuntini CR 14* (SPF, USJ): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. aff. hyacinthina***: PER, Madre de Dios, Manu, *Lohmann 642* (MO, MOL): DQ222614, KC914602, DQ222775, XX9999, XX9999; ***B. lilacina*** (A.H. Gentry) L. G. Lohmann: “A” – BOL, Pando, Madre de Dios, *Beck 20381* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – BR, PA, Paraupebas, *Santos 218* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. longiflora*** Cav.: “A” – ECU, Guayas, Guayaquil, *Gentry 10083* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – PER, Tumbes, *Gentry 58338* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. magnifica*** W. Bull: BR, SP, Nova Odessa, *Lohmann 711* (MO, SPF): DQ222636, XX9999, XX9999, XX9999, XX9999; ***B. microcalyx*** G. Mey: “A” – GUI, W Demerara, Mabara Hill, *Steeger 357* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; “B” – SUR, Sipaliwini, *Evans 3198* (MO, NY, U): DQ222629, XX9999, DQ222797, XX9999, XX9999; ***B. neoheterophylla*** L. G. Lohmann: NIC, Jinotega, Wiwili, *Coronado 2919* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; ***B. nocturna*** (Barb. Rodr.) L.

G. Lohmann: "A" – BR, AC, Marechal Taumaturgo, *Lohmann 451* (MO, NY): DQ222641, XX9999, DQ222813, XX9999, XX9999; "B" – BOL, Santa Cruz, Velasco, *Guillén 1262* (NY): XX9999, XX9999, XX9999, XX9999, XX9999; **B. phellosperma** (Hemsl.) L. G. Lohmann: COS, Guanacasta, Bagaces, *Chavarría 1400* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; **B. potosina** (K. Schum. & Loes.) L. G. Lohmann: "A" – MEX, Yucatan, Mérida, *Carnevali 6840* (MO): KC914590, KC914596, KC914614, KC914615, KC914616; "B" – MEX, Chiapas, Ocosingo, *Álvarez 5353* (MO): KC914587, KC914593, KC914608, KC914609, XX9999; **B. prieurii** DC.: "A" – BR, ES, Linhares, *Zuntini 187* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; "B" – BR, ES, Linhares, *Lohmann 651* (MO, CVRD): DQ222615, XX9999, DQ222776, XX9999, XX9999; "C" – BR, AM, Manaus, *Nogueira 159* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; **B. pterocalyx** (Dugand) L. G. Lohmann: COL, Magdalena, *Gentry 55507* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; **B. ramentacea** (Mart. ex DC.) L. G. Lohmann: "A" – BR, PI, Pedro II, *Barros 1894* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; "B" – BR, CE, Aiuaba, *Lemos 283* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; "C" – BR, PB, Curral de Cima, *Lohmann 700* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; **B. sciuripabulum** (Bureau & K. Schum.) L. G. Lohmann: "A" – PER, Madre de Dios, Manu, *Maceda 633* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; "B" – BOL, Cochabamba, *Thomas 1081* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; "C" – PER, Madre de Dios, Manu, *Lohmann 608* (MO, MOL): DQ222571, XX9999, XX9999, XX9999, XX9999; "D" – BR, ES, Linhares, *Zuntini* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; **B. sordida** (Bureau & K. Schum.) L. G. Lohmann: "A" – PER, Loreto, Tamshiyacu, *Gentry 25849* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; "B" – SUR, Sipaliwini, *Hofmann 5363* (MO): XX9999, XX9999, XX9999, XX9999, XX9999; **B. uleana** (Kraenzl.) L.G. Lohmann: "A" – BOL, Santa Cruz, Opisbo, *Nee 39466* (MO, NY, TEX): KC914589, KC914595, KC914613, XX9999, XX9999; "B" – PER, Madre de Dios, Manu, *Lohmann 617* (MO, MOL): DQ222572, KC914601, DQ222709, XX9999, XX9999; **B. aff. uleana** (Kraenzl.) L. G. Lohmann: CR, Puntarenas, *Acosta 826* (INB): XX9999, XX9999, XX9999, XX9999, XX9999.

OUTGROUPS: ***Amphilophium bauhinoides*** (Bureau ex Baill.) L.G. Lohmann: BR, ES, Linhares, *Lohmann 655* (SPF): DQ222586, KC914599, DQ222734, XX9999, XX9999; ***A. elongatum*** (Vahl) L.G. Lohmann: 0, *Lombardi 2433* (BHCB, MO):

DQ222578, XX9999, DQ222720, XX9999, XX9999; *A. frutescens* (DC.) L. G. Lohmann: BR, PB, Rio Tinto, *Lohmann 695* (SPF): DQ222581, XX9999, DQ222724, XX9999, XX9999; *A. paniculatum* (L.) Kunth: PER, Madre de Dios, Manu, *Lohmann 609* (MO): DQ222533, XX9999, DQ222656, XX9999, XX9999; *Anemopaegma chamberlaynii* (Sims) Bureau & K. Schum.: BR, ES, Linhares, *Zuntini 204* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999; *A. foetidum* Bureau & K. Schum.: BR, AM, Ducke, *Lohmann 35* (INPA, MO, SPF): XX9999, XX9999, XX9999, XX9999, XX9999; *A. robustum* Bureau & K. Schum.: BR, AM, Ducke, *Apostolo 126* (INPA): DQ222538, KC914598, DQ222663, XX9999, XX9999; *Mansoa difficilis* (Cham.) Bureau & K. Schum.: BR, ES, Linhares, *Lohmann 662* (CVRD, SPF): DQ222598, KC914600, DQ222752, XX9999, XX9999; *M. onohualcoides* A.H. Gentry: BR, ES, Linhares, *Zuntini 276* (CVRD, SPF): XX9999, XX9999, XX9999, XX9999, XX9999; *M. standleyi* (Steyerm.) A.H. Gentry: PER, Madre de Dios, Manu, *Lohmann 638* (MO): DQ222603, XX9999, DQ222757, XX9999, XX9999; *Pyrostegia venusta* (Ker Gawl) Miers: BR, SP, E.S. Pinhal, *Zuntini 281* (SPF): XX9999, XX9999, XX9999, XX9999, XX9999.

Appendix 2. Morphological matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Amphilophium bauhinioides</i>	0	0	0	1	1	3	0	0	0	0	1	0	0	1	0	2	1	0	-	0
<i>A. elongatum</i>	0	0	0	1	1	3	0	0	0	1	2	0	0	1	1	0	0	2	1	0
<i>A. frutescens</i>	0	3	1	1	1	1	1	1	0	1	1	0	0	1	1	0	1	0	-	0
<i>A. paniculatum</i>	0	3	1	1	1	0	-	-	0	1	2	0	0	1	1	0	1	2	0	0
<i>Anemopaegma chamberlaynii</i>	0	0	0	1	0	1	0	1	0	0	2	0	0	0	1	0	1	0	-	-
<i>A. foetidum</i>	1	0	0	0	1	0	-	-	0	0	2	0	0	0	1	0	1	0	-	-
<i>A. robustum</i>	0	0	0	0	0	?	?	1	0	0	2	0	0	0	0	0	1	2	0	0
<i>Bignonia aequinoctialis</i>	0	12	0	1	0	1	0	1	1	0	1	?	0	?	0	0	0	2	1	0
<i>B. binata</i>	0	0	0	0	0	2	0	0	1	0	1	1	0	0	0	0	0	1	-	-
<i>B. aff binata</i>	0	1	2	1	0	2	0	0	1	0	1	1	0	0	0	0	0	1	-	-
<i>B. bracteomana</i>	0	12	0	1	1	2	0	1	0	1	1	1	0	1	0	1	0	2	0	1
<i>B. callistegioides</i>	0	0	0	1	0	2	0	0	1	0	1	1	0	0	0	0	0	1	-	-
<i>B. campanulata</i>	0	2	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	2	1	0
<i>B. capreolata</i>	0	2	0	1	1	12	0	1	1	0	1	1	0	0	2	0	1	1	-	-
<i>B. convolvuloides</i>	1	2	1	1	0	3	0	0	1	0	1	?	0	0	0	0	0	1	-	-
<i>B. corymbosa</i>	0	1	0	0	0	1	1	1	0	0	1	1	0	0	0	3	0	23	1	0
<i>B. costata</i>	0	2	0	1	0	2	0	0	1	0	1	1	0	0	0	0	0	1	?	-
<i>B. cuneata</i>	0	0	0	0	0	23	0	0	1	0	0	?	0	0	0	0	0	1	-	-
<i>B. decora</i>	0	2	2	1	1	1	1	0	1	0	1	1	0	1	0	0	0	2	1	0
<i>B. diversifolia</i>	0	2	2	1	1	1	1	0	0	0	1	?	1	1	0	0	0	2	1	0
<i>B. hyacinthina</i>	0	2	2	1	1	1	1	1	1	1	12	?	0	1	0	0	0	2	1	0
<i>B. aff hyacinthina</i>	0	2	2	?	1	1	?	1	1	1	1	?	0	1	0	0	0	2	1	0
<i>B. lilacina</i>	0	0	0	1	0	2	0	0	1	0	1	?	0	1	0	0	0	2	1	0
<i>B. longiflora</i>	1	0	0	0	1	1	0	1	0	0	1	?	0	0	0	0	0	2	0	0
<i>B. magnifica</i>	0	0	0	1	1	1	1	1	1	0	1	?	0	0	0	0	1	3	1	0
<i>B. microcalyx</i>	0	2	0	0	1	0	0	0	0	0	12	?	0	0	0	1	0	0	-	-

Appendix 2. Morphological matrix (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>B. neoheterophylla</i>	0	1	0	0	1	3	0	0	1	0	12	?	1	1	0	0	0	0	-	-
<i>B. nocturna</i>	0	0	0	0	1	0	0	0	0	0	1	?	1	0	0	0	1	2	1	0
<i>B. phellosperma</i>	0	0	0	0	0	1	1	0	1	0	1	?	0	0	0		0	2	0	0
<i>B. potosina</i>	0	2	12	1	0	2	0	1	1	0	1	1	0	0	0	0	0	0	-	-
<i>B. prieurii</i>	0	0	0	1	1	1	0	1	1	1	2	?	0	1	0	0	0	2	1	0
<i>B. pterocalyx</i>	0	12	1	1	0	23	0	1	1	0	1	?	0	0	0	0	0	1	-	-
<i>B. ramentacea</i>	1	2	1	1	0	3	0	0	1	0	1	?	0	0	0	0	0	1	-	-
<i>B. sciuripabulum</i>	0	2	2	1	0	2	0	0	0	0	1	?	0	0	0	0	0	0	-	-
<i>B. sordida</i>	0	12	0	1	0	2	0	1	0	1	1	?	0	0	0	1	0	1	0	1
<i>B. uleana</i>	0	12	0	1	0	12	0	0	1	0	1	?	0	1	0	0	0	2	0	0
<i>B. aff uleana</i>	0	0	0	0	1	0	-	0	?	0	1	1	0	1	0	0	0	2	1	0
<i>Mansoa difficilis</i>	0	0	0	1	1	3	0	0	0	0	2	0	1	0	1	0	1	0	-	-
<i>M. onohualcoides</i>	0	0	0	1	1	3	0	0	0	0	2	0	1	0	1	0	0	0	-	-
<i>M. standleyi</i>	0	0	0	0	1	3	0	0	0	0	1	0	1	0	1	0	0	2	0	0
<i>Pyrostegia venusta</i>	0	3	1	0	1	3	0	0	0	0	2	0	0	0	1	0	1	2	1	0

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
<i>Amphilophium bauhinioides</i>	0	1	0	3	0	0	?	?	1	0	2	2	0	12	1	0	1	1	0	0	0	2	1
<i>A. elongatum</i>	0	1	0	0	2	3	0	?	0	0	0	2	0	2	1	0	1	1	0	1	0	2	2
<i>A. frutescens</i>	0	0	0	0	2	0	0	2	1	0	0	2	0	2	1	0	1	1	0	?	1	0	-
<i>A. paniculatum</i>	0	1	0	3	0	1	?	0	0	0	2	2	0	2	1	0	1	1	0	0	0	2	0
<i>Anemopaegma chamberlaynii</i>	2	0	0	0	2	3	1	0	1	0	3	?	0	1	1	0	2	1	0	0	0	2	1
<i>A. foetidum</i>	2	0	0	0	2	3	0	0	1	0	3	?	0	1	1	0	2	1	0	1	0	2	0
<i>A. robustum</i>	2	1	0	0	2	3	0	1	1	0	2	2	0	1	0	0	2	1	0	0	?	?	0
<i>Bignonia aequinoctialis</i>	0	1	1	0	?	0	?	?	1	0	3	1	0	1	0	1	?	0	0	?	0	2	?
<i>B. binata</i>	0	0	1	0	0	0	0	2	1	0	?	?	1	0	0	1	1	1	1	0	0	1	2
<i>B. aff binata</i>	2	0	1	0	2	0	0	2	1	0	0	1	1	0	0	1	2	1	1	0	1	0	-
<i>B. bracteomana</i>	1	1	1	0	2	0	0	0	1	0	1	0	0	1	0	1	0	0	2	0	0	2	2
<i>B. callistegioides</i>	0	0	1	0	0	0	0	1	1	0	?	?	1	0	0	1	1	1	1	0	1	0	-
<i>B. campanulata</i>	0	1	0	0	0	0	3	0	1	0	?	?	1	0	0	1	1	1	1	0	0	1	2
<i>B. capreolata</i>	2	0	0	0	0	2	1	1	1	1	?	?	0	1	0	0	0	0	0	0	0	2	1
<i>B. convolvuloides</i>	0	0	1	0	1	0	0	0	1	0	0	2	1	0	0	1	1	1	1	0	0	1	1
<i>B. corymbosa</i>	2	1	1	2	2	0	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0	2	2
<i>B. costata</i>	0	0	1	0	1	0	0	1	0	0	0	2	0	1	1	1	?	?	?	?	?	?	?
<i>B. cuneata</i>	2	0	1	0	1	0	0	1	1	0	?	?	1	0	0	1	1	1	1	0	?	?	?
<i>B. decora</i>	0	1	1	1	1	0	0	0	1	0	3	?	0	1	1	1	0	0	0	0	0	2	1
<i>B. diversifolia</i>	2	1	1	0	1	0	0	2	1	0	3	?	0	1	?	1	?	0	0	?	0	2	?
<i>B. hyacinthina</i>	0	1	1	0	0	4	2	0	1	1	1	0	0	1	1	1	1	1	2	0	0	2	2
<i>B. aff hyacinthina</i>	0	1	1	0	0	4	2	0	1	?	?	?	0	1	1	1	?	?	?	?	?	?	?
<i>B. lilacina</i>	0	1	1	0	2	0	0	0	1	0	3	?	0	1	1	1	1	1	0	1	0	2	2
<i>B. longiflora</i>	2	1	0	1	2	2	1	0	1	1	4	3	0	1	0	0	0	0	0	0	0	2	1
<i>B. magnifica</i>	0	1	0	1	1	0	0	0	1	0	4	3	0	1	0	0	0	0	0	0	0	2	1
<i>B. microcalyx</i>	2	0	1	0	2	0	0	0	1	0	1	0	0	1	1	1	?	?	?	?	?	?	?

Appendix 2. Morphological matrix (continued)

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
<i>B. neoheterophylla</i>	2	1	1	0	2	0	0	0	1	0	0	4	0	1	0	1	0	0	0	0	0	2	1
<i>B. nocturna</i>	0	1	0	1	2	1	1	0	1	1	4	2	0	1	1	0	1	1	0	1	0	2	12
<i>B. phellosperma</i>	0	0	1	2	2	0	0	0	1	0	?	?	0	1	0	1	2	1	0	0	1	0	-
<i>B. potosina</i>	2	0	1	0	2	0	0	1	1	0	0	1	0	1	?	1	1	0	0	0	0	2	12
<i>B. prieurii</i>	0	1	1	0	0	4	2	0	1	0	?	?	0	1	1	1	1	1	2	0	0	2	2
<i>B. pterocalyx</i>	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	2
<i>B. ramentacea</i>	0	0	1	0	1	0	0	0	1	0	0	2	1	0	0	1	1	1	1	0	0	1	1
<i>B. sciuripabulum</i>	0	1	0	0	0	0	0	0	1	0	0	2	1	0	0	1	1	1	1	0	0	1	2
<i>B. sordida</i>	2	1	1	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	2	0	0	2	2
<i>B. uleana</i>	0	1	1	0	1	0	0	1	1	0	0	2	1	0	0	1	1	1	1	0	0	1	2
<i>B. aff uleana</i>	0	1	1	0	1	0	0	2	1	0	?	?	1	0	0	1	1	1	1	0	?	?	?
<i>Mansoa difficilis</i>	2	0	0	0	0	0	0	0	0	0	5	?	0	1	1	0	0	1	2	0	0	2	0
<i>M. onohualcoides</i>	2	1	0	0	1	0	0	1	0	0	5	?	0	1	1	0	0	1	2	?	0	2	0
<i>M. standleyi</i>	2	1	0	0	0	0	0	1	0	0	5	?	0	0	0	0	0	0	0	0	0	2	1
<i>Pyrostegia venusta</i>	1	1	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	2	0

Characters: **1** Habit (0) Liana (1) Shrub; **2** Stems cross-section (0) Cylindrical (1) Sub-quadrangular (2) Quadrangular (3) Hexagonal; **3** Stem projections (0) no (1) ribbed (2) winged; **4** Interpetiolar ridge (0) Absent (1) Present; **5** Prophylls display (0) Caducous (1) Persistent; **6** First Prophylls shape (0) Minute (1) Elliptic to circular (2) Falcate (3) Subulate; **7** Prophylls position (0) Ascending (1) Spreading; **8** Prophylls height (0) sessile (1) Stipitate; **9** Bromeliad-like prophylls (0) Absent (1) Present; **10** Leaf domatia (0) Absent (1) Present; **11** Leaf structure (0) 1 foliolate (1) 2 foliolate (2) 2-3 foliolate; **12** Terminal leaflet abortion (0) Absent (1) Present; **13** Primary venation (0) Pinnate (1) Actinodromous; **14** Tertiary venation (0) Alternate percurrent (1) Opposite percurrent; **15** Tendril (0) simple (1) trifid (2) multifid; **16** Tendril apex (0) simple (1) 2-3-fid (2) disk (3) spatulate (glandular); **17** Tendril persistency (0) Caducous (1) Persistent; **18** Inflorescence structure (0) Raceme (1) Reduced raceme (2) thyrses (3) Compound dichasia; **19** Lateral inflorescence structure (0) simple dichasia (1) compound dichasia; **20** Lateral inflorescence branch (0) pedunculate (1) sessile; **21** Inflorescence position (0) Terminal (1) Lateral (2) Axillary;

22 Number of flowers (0) few (1) many; **23** Synchronous flowering (0) Absent (1) Present; **24** Calyx shape (0) Cupular (1) Tubular (2) Spathaceous; **25** Glands in calyx (0) Absent (1) Scattered (2) Clustered; **26** Corolla color (0) Purple, pink or magenta (1) White (2) Orange / Red (3) Yellow (4) Brownish; **27** Corolla shape (0) Infundibuliform (1) Narrowly infundibuliform (2) Billabiate (3) Campanulate; **28** Corolla - simple trichomes (0) glabrous - glabrescent (1) pubescent (2) sericeous; **29** Corolla - lepidote scales (0) absent (1) present; **30** Androecium position (0) Included (1) Exserted; **31** Pollen apertures (0) Inaperturare (1) 3-4-aperturate (2) zonocolpate (3) periclpate (4) polyporate; **32** Pollen ornamentation (0) Finely reticulate (1) medium reticulate (2) coarse reticulate (3) complex patterns (4) spinulose; **33** Ovary surface (0) Smooth (1) Verrucose; **34** Ovary indument (0) Glabrous (1) Lepidote (2) Pilose / sericeous; **35** Series of ovules per locule (0) Two (1) more than two; **36** Nectariferous disk (0) Developed (1) Undeveloped or absent; **37** Fruit shape (0) linear (1) oblong or elliptical (2) circular; **38** Fruit flatness (0) Flattened (1) Ellipsoid or cylindrical; **39** Fruit surface (0) Smooth (1) Echinata (2) Verrucose; **40** Glands in fruits (0) Absent (1) Present; **41** Seeds texture (0) slim (1) corky; **42** Seed wings (0) no wings (1) one (2) two; **43** Seed wings opacity (0) hyaline (1) translucent (2) opaque.

Supplement 1.

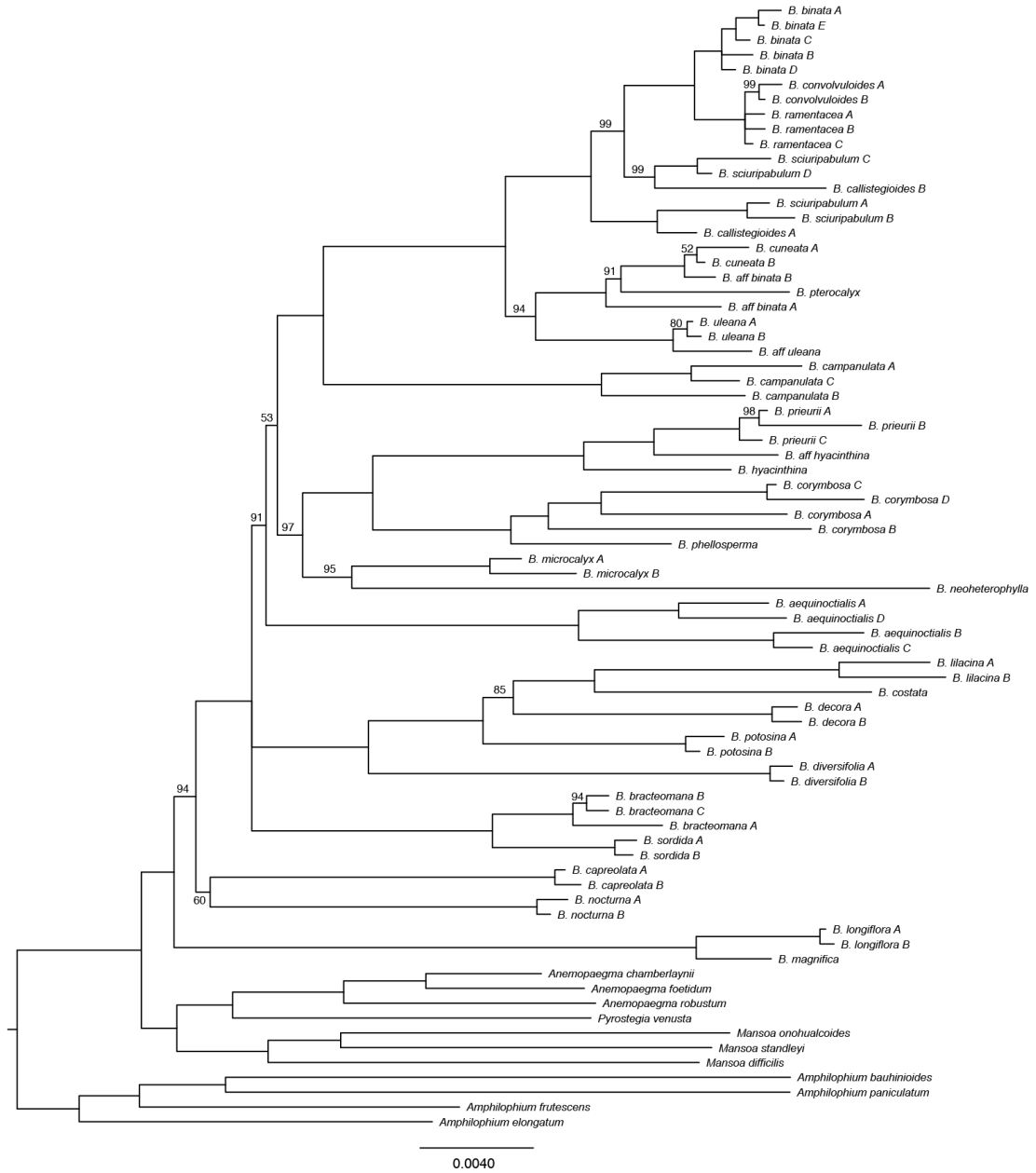


Figure S1: Phylogram of Bayesian analysis from combined data (ndhF + rpl32 trnL + pepC). Values near branches indicate their posterior probability, in percentage; absent values denote 100%.

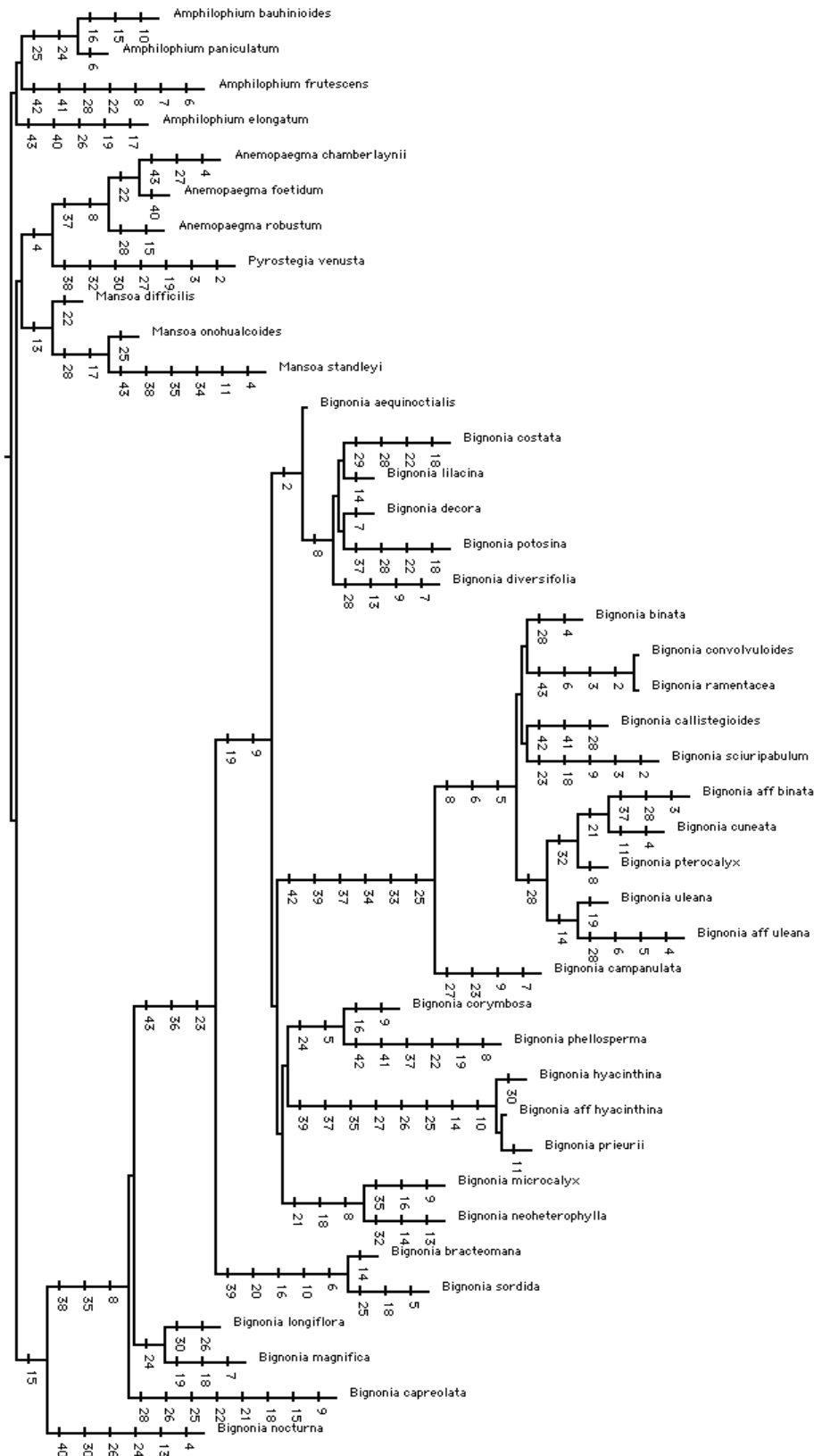


Fig. S2: Morphological characters reconstructed over combined, single accession tree. Characters code according to Appendix 2.

Conclusões

1. O gênero *Bignonia* é monofilético, incluindo o antigo gênero *Macranthisiphon*;
2. São reconhecidas 30 espécies, das quais duas descritas como novas (*B. cararensis* e *B. sanctae-crucis*), uma reestabelecida (*B. noterophila*) e outra sinonimizada (*B. convolvuloides* sinonimizada em *B. ramentacea*);
3. Quatro subgêneros (*Adiscae*, *Bignonia*, *Osmhydrophra* e *Saritaea*) e seis seções (*Clytostoma*, *Macrostipulae*, *Mussatia*, *Phryganocydia*, *Potamoganos* e *Roentgenia*) são propostos baseados nos dados filogenéticos e morfológicos;
4. O uso de sequenciamento tradicional (Sanger) aliado ao sequenciamento em larga escala levou à reconstrução de uma filogenia robusta para o gênero;
5. Os dados morfológicos e filogenéticos auxiliaram na delimitação das espécies mas também apontaram a possível influência de processos de hibridação e introgressão em eventos de diversificação em alguns clados, especialmente nas seções *Clytostoma* e *Mussatia*.