



Deciphering the Neotropical *Bignonia binata* species complex (Bignoniaceae)

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Abstract

Bignonia is a genus of 28 species of Neotropical lianas. Most species are clearly characterized by morphological features, monophyletic and narrowly distributed. However *Bignonia binata* is polymorphic, polyphyletic and broadly distributed, from Mexico to Argentina. A detailed morphological survey of *B. binata* in the light of geographical and ecological data in its current circumscription recovered two clearly distinct morphological groups of plants. One group is found in Argentina, Paraguay and the Atlantic forest of Brazil, and characterized by non-winged stems, usually terminal inflorescences, usually non-glandular calyces, pantoaperturate pollen, narrowly elliptic fruits, and 1-winged seeds. The second group occurs in Central America and Amazonia and is characterized by winged young stems, usually axillary inflorescences, glandular calyces, inaperturate pollen, widely elliptic to circular fruits, and wingless seeds. The first group of plants corresponds to *B. binata* and the second group is recognized as another species, *B. noterophila*. Synonyms, morphology, distributions, and ecology are detailed for these newly circumscribed species. Lectotypes are designated for *B. noterophila* and several synonyms: *Adenocalymma ocositense*, *Arrabidaea schumanniana*, and *Petastoma laurifolium*.

Keywords: Neotropical flora, Palynology, Species delimitation, Species complex

Introduction

Bignonia Linnaeus (1753: 622) is a monophyletic lineage that was recently re-circumscribed (Lohmann & Taylor 2014) to now also include nine previously accepted genera: *Clytostoma* Miers ex Bureau (1868: 353), *Cydista* Miers (1863: 191), *Macranthisiphon* Bureau ex Schumann (1894: 219), *Mussatia* Bureau ex Baillon (1891 [1888]: 32), *Osmhydrophora* Rodrigues (1891: 49), *Phryganocydia* Mart. ex Bureau (1872: 18), *Potamogonos* Sandwith (1937: 220), *Roentgenia* Urban (1916: 747) and *Saritaea* Dugand (1945: 262). Under the new circumscription, *Bignonia* is characterized by eight phloem wedges in the stems (easily seen in cross-section), usually 2-foliolate leaves with simple tendrils, and opaque seed wings (Lohmann & Taylor 2014). While most species of *Bignonia* are morphologically well defined and narrowly distributed, *B. binata* Thunberg (1821: 35) as it has been recognized is polymorphic and very broadly distributed, ranging from Mexico to northern Argentina (Gentry 2009).

Thunberg (1821) described *B. binata* based on a collection made by Freyreiss, from an unknown locality somewhere in southeastern Brazil. The identity of *B. binata* was not clear at that time and the name was seldom used. More than two decades later, de Candolle described *Bignonia noterophila* Mart. ex Candolle (1845: 148) based on a collection from Martius made in the flooded forests of Pará in northern Brazil. *Bignonia noterophila* was later transferred into *Clytostoma* by Bureau and Schumann (1896), who recognized a more widely distributed *Clytostoma noterophilum* (Mart. ex DC.) Bureau & Schumann (1896: 153) that ranged from French Guiana to Rio Grande do Sul, in southern Brazil. Their circumscription of *C. noterophilum* led to the recognition of a morphologically variable taxon that occupied many different habitats beyond just flooded forests. Sandwith (1937) later analyzed Thunberg's original collection of *B. binata* and realized that this was an earlier name for the plants included in *C. noterophilum*. He therefore published the combination *Clytostoma binatum* (Thunb.) Sandwith (1937: 231) and placed *B. noterophila*, *B. umbellulata* Candolle (1845: 148), and *B. purpurea* Lodd. ex Hooker (1869: t. 5800) as synonyms. Following the broad circumscription of Sandwith (1937), additional species were later also included within the circumscription of *B. binata* by subsequent workers (e.g., Gentry 1973; Macbride 1961; Standley & Williams 1974). More recently, *Clytostoma* was synonymized under *Bignonia* and *Bignonia binata* became again the accepted name for this broadly circumscribed species (Lohmann & Taylor 2014).

Despite the wide geographic distribution and the morphological and ecological variation observed in *B. binata*, its broad circumscription has never been questioned. However this broadly circumscribed species, unusual in Bignoniaceae, has emerged as polyphyletic in a recent molecular phylogenetic study (Zuntini & Lohmann, unpub. data). While hybridization, lineage sorting and other genetic events can lead to polyphyletic species (e.g., Majure *et al.* 2012; Soltis & Soltis 2009), molecular phylogenies have recently provided key insights into the identification of cryptic taxa (e.g., Govindarajulu *et al.* 2011). The molecular polyphyly of *B. binata* coupled with the wide morphological and ecological variation suggest that multiple taxa might currently be mixed under a single name and that this circumscription needs to be further investigated.

We conducted a detailed morphological analysis of the plants now included in *Bignonia binata*, also referred to as the *Bignonia binata* species complex, and analyzed these morphological data together with geographic distribution and ecological preferences. Because pollen morphology was shown to be variable among species of *Bignonia* (Gentry & Tomb 1979), a palynological study was also conducted.

Methods

We examined specimens from the following herbaria: BA, BM, F, G, GH, K, M, MBM, MG, MICH, MO, NDG, NY, P, PH, S, SPF, UPS, US (acronyms following Thiers 2015). Morphological terms follow Lohmann & Taylor (2014) and Radford *et al.* (1974), with rare conditions presented within parentheses. The descriptions here are based on the genus description for *Bignonia* presented by Lohmann & Taylor (2014: 416) and do not repeat the genus-level characters. To look for useful palynological characters, flowering buds of selected specimens (Appendix 1) were dissected and the whole content of a single theca was spread in a stub. Stubs were sputter-coated with Au/Pd alloy on a Denton Desk V Cold Sputter Coater set at 35 mAmps for 120 seconds. Micrographs were obtained on a JEOL NeoScope JCM-5000 scanning electron microscope, using 10kV under high vacuum. The pollen terminology used here follows Hesse *et al.* (2009) and Gentry & Tomb (1979). Selected images of pollen and representative specimens are available at TROPICOS® (2015).

Results and discussion

The morphological analyses revealed many variable and overlapping characters, such as size and indument of leaves and corollas, which helps explain why *B. binata* has been treated as a single polymorphic species for more than a century. Nevertheless, two morphologically distinct groups are clearly distinguishable among the plants now classified in *B. binata*. The first group of plants is found in the Atlantic Forest from eastern Brazil through Paraguay to northern Argentina (Fig. 1). Individuals from this morphological group can be recognized by their non-winged stems, usually terminal inflorescences, non-glandular calyces or calyces with just a couple of glands, narrowly elliptic fruits, and 1-winged seeds (Table 1, Fig. 2-A–E). The second morphological group occurs in Central America and Amazonia, and is characterized by winged young stems, usually axillary inflorescences, regularly glandular calyces, widely elliptic to circular fruits, and wingless seeds (Fig. 2-G–K).

The morphological features of this first group of plants match the characters of *Bignonia binata*. It is not completely clear where Georg W. Freyreiss collected the type specimen of *B. binata*, but it is known that he travelled to Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro between 1813 and 1818 (Urban 1906: 21), where the first group is distributed. On the other hand, the morphological features that characterize the second group of plants match the characters of *B. noterophila*, and its type was collected within the area where this second group of plants is found. Pollen morphology also supports the separation of these two groups, with pantoaperturate, coarsely reticulate or rarely medium-reticulate pollen grains found exclusively in the *B. binata* group (Fig 2-F) and inaperturate, medium-reticulate pollen grains found exclusively in the *B. noterophila* group (Fig 2-L).

In addition to distinct morphologies and geographic distributions, these two groups of plants also have distinctive and different ecologies. The *Bignonia noterophila* group's wingless and corky seeds are likely hydrochoric. These plants are restricted to river banks, riparian forests and other vegetation types associated with water bodies, being particularly abundant in flooded forests (Gentry 1976, as *Clytostoma binatum*). *Bignonia binata*, on the other hand, has winged thin-textured seeds that are likely wind-dispersed, and is found in evergreen, non-flooded forests (A. Zuntini, pers. obs.).

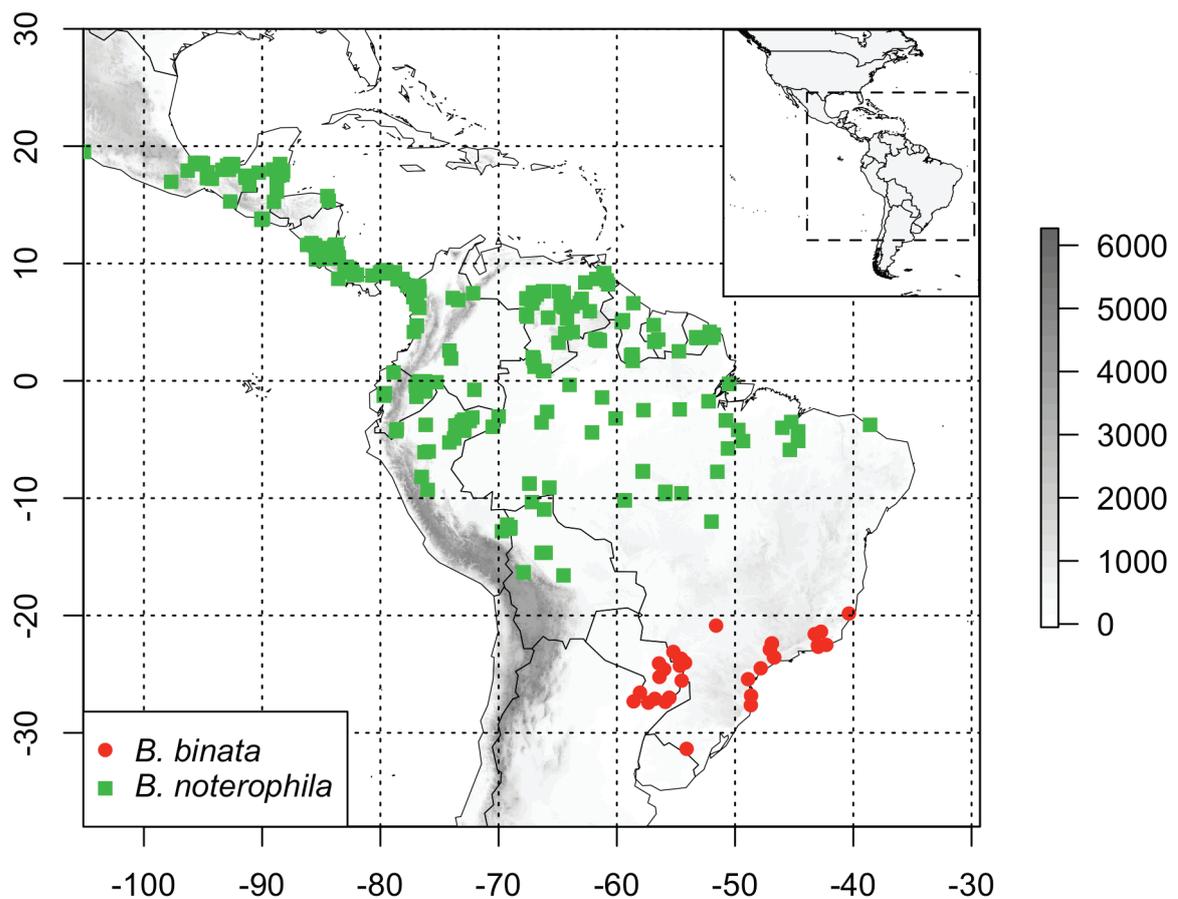


FIGURE 1. Distribution of *Bignonia binata* Thunb. (red circles) and *B. noterophila* Mart. ex DC. (green squares). Elevation in meters, following the scale presented on the right.

TABLE 1. Morphological comparison between *Bignonia binata* Thunb. and *B. noterophila* Mart. ex DC. Terms within parentheses denote rare conditions; non-overlapping characters are marked in bold.

Character	<i>B. binata</i>	<i>B. noterophila</i>
Winged stems	Never	When young
Leaflet base	Rounded	Cuneate (rounded or oblique)
Inflorescence position	Terminal (axillary)	Axillary (terminal)
Glands in calyx	None (few)	Many (few)
Pollen ornamentation	Coarse reticulate (medium reticulate)	Medium reticulate
Pollen aperture	Pantoaperturate	Inaperturate
Fruit shape	Oblong to narrowly elliptic	Widely elliptic to circular
Seed wings	One	None
Hypothetical seed dispersal	Anemochory	Hydrochory
Habitat	Various habitats in Evergreen forest	Riparian and water-associated habitats in tropical humid forest
Distribution	Atlantic forest	Central America and Amazonia

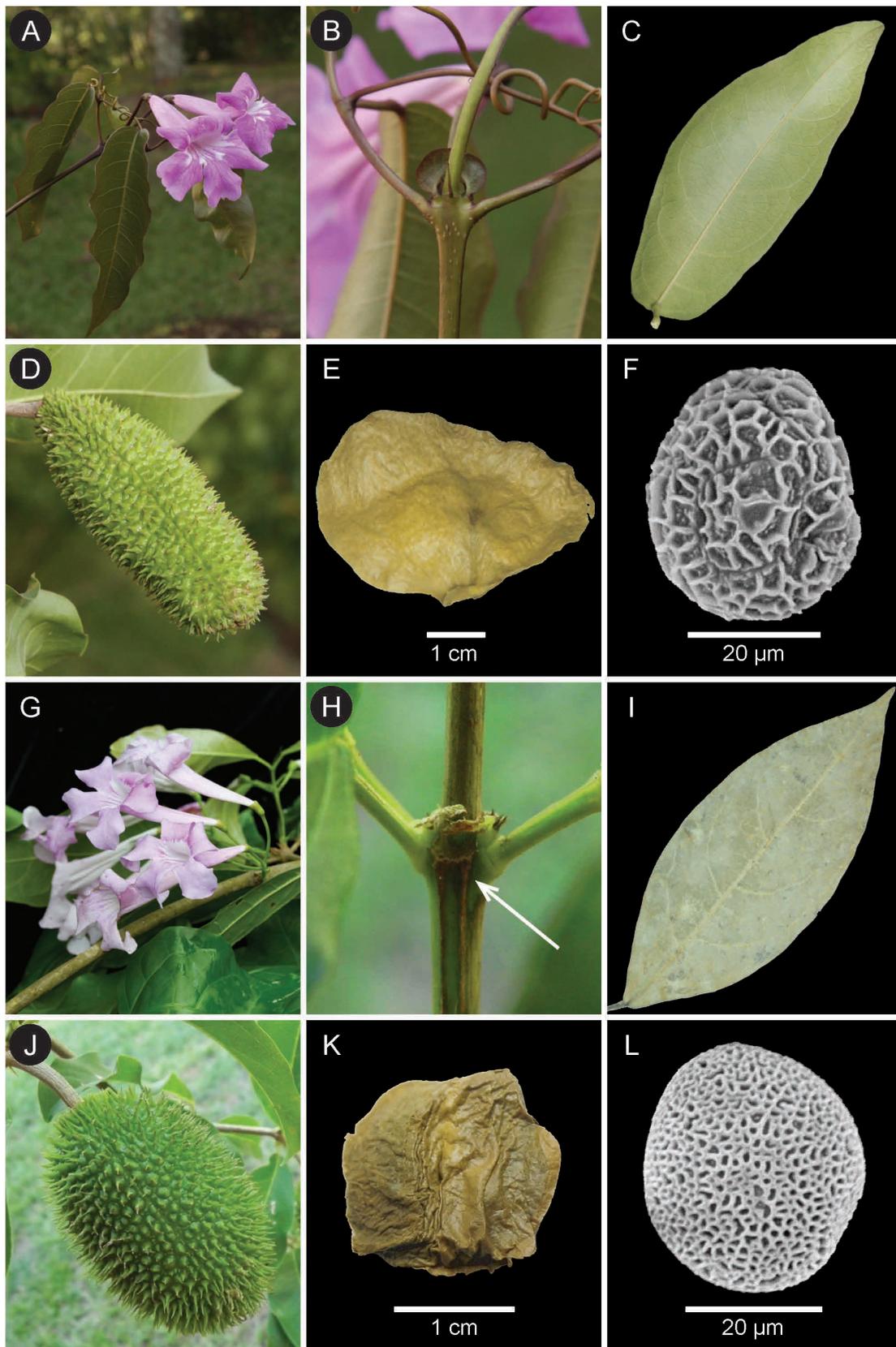


FIGURE 2. Key characters that distinguish *Bignonia binata* Thunb. from *B. noterophila* Mart. ex DC. A–F: *B. binata*. A. Terminal inflorescence. B. Young branch node. C. Leaflet. D. Fruit. E. Winged seed. F. Pantoaperturate (central C-shape) pollen grain. G–L: *B. noterophila*. G. Axillary inflorescence. H. Young winged branch node; arrow indicates branch wing. I. Leaflet. J. Fruit. K. Wingless seed. L. Inaperturate pollen grain. A–D: Zuntini 355 (SPF); E: Hoenhe s.n. (SPF-46408); F: Pedersen 6546 (MO), G: Stevens 31475 (MO); H, J: Zuntini CR3 (USJ); I: Evans 2355 (SPF); K: Gentry 8478 (SPF); L: Steyermark 114851 (MO). Photo G was taken by Olga Martha Montiel, while all other photos were taken by ARZ.

Based on morphology, distribution, ecology and molecular phylogenetic differences the two groups of plants currently included in *B. binata*, we here reestablish *B. noterophila* as a separate species and make the necessary taxonomic adjustments. Below we provide full descriptions for the two newly circumscribed taxa, and assign the previous synonyms of *B. binata* to the correct taxa with two heterotypic synonyms accepted for *B. binata* and seven heterotypic synonyms assigned to *B. noterophila*. With the reestablishment of *B. noterophila*, *Bignonia* now comprises 29 species.

Taxonomy

1. *Bignonia binata* Thunberg (1821: 35) ≡ *Clytostoma binatum* (Thunb.) Sandwith (1937: 231)

Type:—BRAZIL. S.loc., Jan–Feb [1813–1818], *G.W. Freyreiss s.n.* (holotype: UPS-14225 image!)

Bignonia umbellulata Candolle (1845: 148)

Type:—BRAZIL. S.loc., 1832, *J. Lhotsky s.n.* (holotype: G-DC (two numbered sheets) [G-00133285, G-00133378] image!)

Bignonia eximia Morong in Morong & Britton (1892: 187)

Type:—PARAGUAY. On the highway between Villa Rica and Escoba, 30 January 1899, *T. Morong 595* (holotype: NY [00579080]!)

Description: Lianas. **Stems** cylindrical, not winged, not striate, with lenticels, with interpetiolar ridge, minutely pubescent or pubescent when young at least at nodes, sparsely lepidote; foliaceous prophylls caducous, falcate, ascending, stipitate, asymmetrical, 1.3–5.4 × 0.8–2.6 mm, ciliate, sparsely lepidote, with few glands at abaxial surface; bromeliad-like prophylls present. **Leaves** (1–)2-foliolate; petiole 7.1–26.1 mm, minutely pubescent throughout or just above, sparsely lepidote; petiolules 7.1–18.8 mm, minutely pubescent throughout or just above, sparsely lepidote; blades concolorous (discolorous), sub-chartaceous to chartaceous (sub-coriaceous), symmetrical (slightly asymmetrical), narrowly elliptic to elliptic, acute to acuminate apically, rounded basally, 6.4–14.1 × 2.3–5.3 cm, on adaxial surface puberulent above midvein, very sparsely lepidote, without glands (few at base), on abaxial surface without simple trichomes, sparsely lepidote, with few glands at base or scattered; venation pinnate, with tertiary veins alternate percurrent; tendrils rarely present, simple, without simple trichomes, sparsely lepidote. **Inflorescences** reduced racemes, 2–8-flowered, umbelliform, terminal (axillary), minutely pubescent, sparsely lepidote, with primary axis 0–2.0 mm long; bracts caducous, linear, 1.0–4.0 × 0.2–0.6 mm, ciliate, not lepidote, without glands; pedicels 12.1–36.2 mm, puberulent, sparsely lepidote. **Flowers** with calyx cupular, 5-toothed, membranous, (2.5–) 4.0–6.2 × 4.3–7.1 mm wide at apex, ciliate, moderately lepidote, with few scattered glands (no glands), teeth 0.4–1.3 mm; corolla purple (white) outside, white inside, infundibuliform, membranous, (26.5–) 54.4–68.6 (–85.3) mm, externally sericeous, sparsely to moderately lepidote, internally pubescent at lobes, moderately lepidote at lobes, with shortly stipitate glandular trichomes at base, tube (23.1–) 39.5–51.4 × (1.8–) 3.9–5.3 mm wide at base and (9.0–) 12.5–18.9 mm wide at apex, lobes circular (sub-circular), (5.1–) 11.5–19.2 × (5.5–) 8.5–18.2 mm; androecium didynamous, with stamens included, the longest (10.5–) 17.5–20.9 mm, the shortest (6.8–) 10.9–15.1 mm, without simple trichomes (puberulent), not lepidote, with stipitate glandular trichomes at base, thecae 2.2–3.6 mm, staminode 2.5–4.2 mm; gynoecium (20.7–) 29.3–37.0 mm, ovary cylindrical, verrucose, without simple trichomes, not lepidote; nectariferous disk reduced. **Fruits** inflated, oblong, 7.1–10.3 × 2.5–3.1 wide × 0.8–2.1 cm thick, moderately echinate, without simple trichomes, not lepidote, spines cylindrical, 3.0–5.1 mm. **Seeds** brown, thin, transversally elliptic, asymmetrical, 14.1–16.9 × 19.9–26.5 mm, with one opaque wing; seed body lenticular, 1.3–2.4 mm thick.

Distribution:—*Bignonia binata* is found in evergreen forests in **Argentina** (Corrientes, Misiones), **Brazil** (Espírito Santo, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo) and **Paraguay** (Caaguazú, Canindeyú, Itapua, Misiones, Ñeembucú, Paraguari), from sea level to 80 m (Fig. 1).

2. *Bignonia noterophila* Mart. ex Candolle (1845: 148) ≡ *Clytostoma noterophilum* (Mart. ex DC.) Bureau & Schumann (1896: 153).

Lectotype (designated here):—BRAZIL. Pará: Santarém, in sylvis inundatis, 18–23 September 1819, *C.F.P. von Martius s.n.* (M [M0086398] image! as F-Neg 20458 at MO-1692936; isolectotypes: M [M0086399] image!, M [M0086400] image!).

Adenocalymma ocositense Smith (1893: 209) ≡ *Petastoma ocositense* (Donn. Sm.) Kraenzlin (1921: 61) ≡ *Clytostoma ocositense* (Donn. Sm.) Seibert (1940: 414), **syn. nov.**

Lectotype (designated here):—GUATEMALA. Quezaltenango, Ocosito river, 250 ft., April 1892, *J.D. Smith 2688* (US-1322492; isolectotypes GH [GH00091821] image!, K [K000449437] image!, M [M0175853] image!, NY [NY00313047] image!, US-47668)

Bignonia purpurea Lodd. ex Hooker (1869: t. 5800) ≡ *Clytostoma purpureum* (Lodd. ex Hook.f.) Rehder in Bailey (1914: 806).

Holotype:—UNITED KINGDOM, Cultivated in Liverpool Botanical Garden, s.d., s. coll. (K-Hooker [K000449511] image!).

Arrabidaea schumanniana Huber (1906: 606), **syn. nov.**

Lectotype (designated here):—PERU. Loreto, Canchahuaya, 28 October 1898, *J.E. Huber s.n.* (MG-1387, excluding fruits and seeds, image!)

Clytostoma isthmicum Pittier (1917: 257, t. 106), **syn. nov.**

Type:—PANAMA. Canal Zone: along the Trinidad River, near sea level, 19 July 1911, *H.F. Pittier 4008* (holotype US-679092 image!; isotypes NY [NY00328758]!, US-679093 image!)

Petastoma laurifolium Kraenzlin (1921: 58), **syn. nov.**

Lectotype (designated here):—BOLIVIA. Beni, Junction of rivers Beni and Madre de Dios, August 1886, *H.H. Rusby 1144* (K image!, isolectotype MICH-1115833 image!)

Petastoma multiglandulosum Benth. ex Kraenzlin (1921: 58), **syn. nov.**

Lectotype (designated by Gentry 1973: 826):—BOLIVIA. Beni. Junction of rivers Beni and Madre de Dios, August 1886, *H.H. Rusby 1145* (K [K000449470] image!; isolectotypes MICH-1115834 image!, MO-1998969!, NY [02256157, 02256158, 02256161]!).

Clytostoma elegans Standley (1935: 86), **syn. nov.**

Type:—BELIZE. Toledo. Rio Grande, river bank, 250 ft., 10 March 1933, *W.A. Schipp 1127* (holotype: F-669152 image!, as negative at MO-1183675!; isotypes: BM [BM000551257] image!, GH (two numbered sheets) [GH00091973, GH00091974] image!, K [K000449436] image!, MICH-1115828 image!, MO (two numbered sheets) MO-1040196!, MO-1040197!, NY [NY00111334]!, S04-3482 image!)

Description: Lianas. **Stems** circular or sub-quadrangular, winged when young, striate, with lenticels (without lenticels), with or without interpetiolar ridges, without simple trichomes or minutely pilose, sparsely lepidote; foliaceous prophylls caducous, triangular or falcate, ascending, sessile, symmetrical or slightly asymmetrical, 1.8–4.0 mm × 0.8–2.9 mm, ciliate (without simple trichomes), not lepidote, with few to many glands at apex of abaxial surface; bromeliad-like prophylls present. **Leaves** (1–)2-foliolate; petiole 4.7–23.7 mm, without simple trichomes or minutely glabrescent, sparsely lepidote; petiolules 3.9–18.0 mm, without simple trichomes or minutely glabrescent, sparsely lepidote; blades concolorous to discolorous, chartaceous to sub-coriaceous, asymmetrical (slightly asymmetrical), elliptic to narrowly elliptic, acuminate to long acuminate (acute) apically, cuneate (rounded or oblique) basally, 5.8–25.0 × 2.6–8.9 cm, on adaxial surface without simple trichomes (minutely pubescent above midvein), very sparsely to sparsely lepidote,

without glands or few at base or scattered, on abaxial surface without simple trichomes, sparsely lepidote, with few glands at base or scattered; venation pinnate, with tertiary veins alternate percurrent; tendrils rarely present, simple, without simple trichomes, sparsely lepidote. **Inflorescences** reduced racemes, 2–4-flowered, umbelliform, axillary, without simple trichomes or minutely pilose, sparsely lepidote, primary axis 0–1.8 mm long; bracts caducous, linear (ovate), 1.3–4.9 (–7.6) × 0.2–0.4 (–2.5) mm, ciliate, not lepidote, without glands (with many glands); pedicels 5.2–24.6 (–33.3) mm, without simple trichomes or puberulent, sparsely lepidote. **Flowers** with calyx cupular, 5-toothed (truncate), membranous, 3.4–7.4 × 4.0–7.6 mm wide at apex, ciliate (glabrescent), sparsely lepidote, with many (few) glands clustered below teeth, teeth 0–1.0 (–1.8) mm; corolla purple outside, white inside, infundibuliform, membranous, 37.7–89.0 (–108.4) mm, externally sericeous at base and pubescent at tube apex and lobes (entirely sericeous or pubescent only at base), sparsely to moderately lepidote, internally glabrescent to pubescent at lobes, not lepidote (moderately lepidote at lobes), with shortly stipitate glandular trichomes at base, tube 28.7–61.5 (–67.8) × 2.0–4.6 mm wide at base and 14.0–24.9 mm wide at apex, lobes circular (sub-circular), 11.5–32.7 × 8.5–27.6 mm; androecium didynamous, with stamens included, the longest 13.2–22.1 (–31.6) mm long, the shortest 10.2–15.4 (–20.7) mm, without simple trichomes (puberulent), not lepidote, with stipitate glandular trichomes at base; thecae 2.2–3.6 mm; staminode 3.4–7.9 mm; gynoecium 18.0–39.1 (–46.3) mm, ovary cylindrical, verrucose, without simple trichomes, not lepidote; nectariferous disk reduced. **Fruits** inflated, widely elliptic to circular (elliptic), (3.0–) 4.2–9.2 × (2.2–) 2.9–6.4 wide × 0.9–2.0 cm thick, moderately echinate, without simple trichomes, not lepidote, spine cylindrical, 3.7–10.7 mm long. **Seeds** brown, corky, irregularly circular, asymmetrical, 15.2–32.3 × 16.8–29.9 mm, without wings; seed body inflated, 2.1–6.3 mm thick.

Distribution:—*Bignonia noterophila* is found in vegetation associated with water bodies in **Belize** (Belize, Cayo, Toledo), **Bolivia** (Beni, Santa Cruz), **Brazil** (Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Rondônia, Roraima), **Colombia** (Amazonas, Amazonas, Antioquia, Caquetá, Chocó, Meta, Narino, Santander, Valle del Cauca, Vaupes, Vichada), **Costa Rica** (Alajuela, Guanacaste, Heredia, Limón, Puntarenas), **Ecuador** (Esmeraldas, Guayas, Loja, Los Rios, Napo, Pastaza, Zamora-Chinchi), **El Salvador** (Ahuachapán), **French Guiana** (Cayenne), **Guatemala** (Alta Verapaz, Izabal, Petén, Quetzaltenango, San Marcos), **Guyana** (Essequibo, Mazaruni-Potaro), **Honduras** (Gracias a Dios), **Mexico** (Campeche, Chiapas, Jalisco, Oaxaca, Quintana Roo, Tabasco, Veracruz), **Nicaragua** (Carazo, Granada, Río San Juan, Rivas, Zelaya), **Panama** (Bocas del Toro, Canal Area, Colón, Darién, Panamá, San Blas), **Peru** (Huánuco, Loreto, Madre de Dios, Puno, San Martín, Tumbes), **Suriname** (Saramacca, Sipaliwini) and **Venezuela** (Amazonas, Anzoátegui, Apure, Bolívar, Delta Amacuro, Guárico, Sucre, Táchira), from sea level to 560 m (Fig. 1).

Nomenclatural notes:—Candolle (1845) indicated in the protologue of *B. noterophila* that its type was deposited at M. However none of the three specimens located at M were annotated by Candolle. Therefore, the best quality material (M0086398) is here designated as lectotype.

Kraenzlin's types were mostly deposited at B and were destroyed during World War II (Stafleu & Cowan 1981), so typification is required. In the case of *Petastoma multiglandulosum*, Gentry (1973: 826) cited a single specimen from K as the type despite the existence of additional specimens at MICH, MO and NY (not cited in the protologue), therefore lectotypification has been made. In the case of *Petastoma laurifolium*, however, Gentry (1973: 826) cited three specimens (B, K and MICH) but did not designate a lectotype. Among the three specimens listed by Gentry, one was deposited at B and is presumed to be destroyed, another is deposited at MICH (1115833), and the third at K. Given that Kraenzlin more likely saw the material designated at K, this specimen is here designated as lectotype. However, his designated type collection (*Rusby 1144*) is a mixed gathering of two species, as annotated by Sandwith (in sched.). Three of these specimens correspond to *Petastoma laurifolium* and are cited as types of this name here. This same collection number was later cited as the type of *Bignonia brevipes* Rusby (1900: 71), a species now synonymized with *Stizophyllum riparium* (Kunth 1819: 138) Sandwith (1938: 462). The two duplicates that match Rusby's description of *B. brevipes* are deposited at NY (NY00313136) and US (1322428), and should not be considered as isoelectotypes of *P. laurifolium*.

When Smith (1893) published *Adenocalymma* (?) *ocositense*, he only mentioned the collection number but did not designate a holotype. Two sheets were located at US, where Smith's material is deposited (Stafleu & Cowan 1985). Although one sheet (US-47668) was probably mounted earlier than the other (US-1322492), Smith was the collector of this material and clearly saw both specimens given that the description includes elements of both sheets. Both sheets are of equivalent quality and the sheet that was annotated by Smith (US-1322492) is here designated as lectotype.

Arrabidaea schumanniana was described by Huber (1906) based on his own unnumbered collection, deposited at MG. However, his type specimen includes mixed elements of two taxa: (1) the stems, leaves and flowers correspond to *B. noterophila*, and (2) the fruits and seeds are apparently those of a species of *Fridericia* Mart. *Arrabidaea schumanniana* has been considered a synonym of *B. binata* (e.g., Arbo & Lohmann 2008; Brako & Zarucchi 1993), so

we here designate the first part of Huber's collection deposited at MG as the lectotype in order to maintain its current usage (Rec. 9A.4, McNeill *et al.* 2012).

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APPENDIX 1. Vouchers used in palynological study. All specimens are deposited at MO; pollen images are available at TROPICOS®.

Bignonia binata Thunb., Paraguay, Paraguari, *M.M. Arbo 1791*; Brazil, São Paulo, *G. Davidse 10941*; Brazil, Mato Grosso do Sul, *G.G. Hatschbach 48981*; Brazil, Rio de Janeiro, *G.F.J. Pabst 5431*; Paraguay, Misiones, *T.M. Pedersen 6546*.

Bignonia noterophila DC., Brazil, Pará, *A.P. Duarte 7042*; Costa Rica, Heredia, *J.P. Folsom 9305*; Brazil, Roraima, *J.A. Ratter 6204*; Venezuela, Delta Amacuro, *J.A. Steyermark 114851*; Mexico, Veracruz, *T.L. Wendt 3829*.