A REVISION OF GEOFFROEA (LEGUMINOSAE–PAPILIONOIDEAE)

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Geoffroea (Leguminosae–Papilionoideae) has traditionally comprised three species. In this revision the number of species is reduced to two because *G. striata* (Willd.) Morong is considered indistinct from *G. spinosa* Jacq. and is placed in synonymy. No significant morphological variation is found between the five isolated areas of distribution of *G. spinosa*, which occurs in the disjunct seasonally dry tropical forests of South America, and there is certainly no basis for recognizing separate taxa.

Keywords. Biogeography, neotropics, seasonally dry tropical forest.

INTRODUCTION

*Geoffroea* (Leguminosae–Papilionoideae–Dalbergieae) is a small genus of woody plants native to South America. Only one comprehensive taxonomic study has been carried out (Burkart, 1949) in which three species were recognized. There has been much confusion, however, over species delimitation.

*Geoffroea* was first described by Jacquin in 1760 in memory of Claude Joseph Geoffroy, a chemist and botanist with whom he worked in Paris between 1750 and 1752 (Jacquin, 1763). A single species was described, *G. spinosa* Jacq., based on a tree from Brazil seen by Marcgrave and illustrated in Piso and Marcgrave’s *Historia naturalis Brasiliae* (1648). Jacquin’s original publication contained two orthographic variants of the generic name, *Geoffroea* and *Geoffrea*, and subsequent orthographic variants in the literature include *Geoffreaea* L. (1763), *Geoffroya* L. (1774), and *Geoffrea* Stokes (1812) and Sprengel (1818). However, because *Geoffroea* is the most widely recognized spelling and is accepted in *Index Nominum Genericorum* (Farr et al., 1979), it is confirmed here as the correct spelling. Until the works of Bentham (1837, 1839), *Geoffroea* was regularly confused with *Andira*. For example, the first post-Linnaean descriptions of *Andira* were accounts of the medicinal use of the bark and seed of *A. inermis* in Jamaica (Wright, 1777) and *A. surinamensis* in Suriname (Bondt, 1788), and both authors placed their species in *Geoffroea*. *Andira* and *Geoffroea* both have fleshy, drupaceous fruits, which are rare in the Papilionoideae, and therefore it is not surprising that they were confused, despite their floral and vegetative differences.

The name *Robinia striata* was given to a plant found in Caracas, Venezuela by Willdenow in 1803. Morong collected material of the same species in Paraguay in 1890 and considered it to have been placed in the wrong genus. A new combination

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was made by Morong (1892) to Geoffroea striata (Willd.) Morong. Burkart (1949) separated G. spinosa Jacq. and G. striata (Willd.) Morong on the presence or absence of spines and leaflet size, and remarked that these characters seem to be related to habitat; the spiny G. spinosa with smaller leaflets occurs in dry habitats and the spineless G. striata with larger leaflets, near water courses. Wiggin & Porter (1971) in the Flora of the Galapagos Islands included G. striata under G. spinosa, and further doubt has been expressed as to the distinctness of these two species by Prado & Gibbs (1993).

The G. spinosa–G. striata complex occurs only in seasonally dry tropical forests, which are scattered in large disjunct areas across South America (see Fig. 3). No previous work has examined the variation of this species complex in its complete geographical context. This is an important issue because it was shown by Prado & Gibbs (1993) that many genera of woody plants such as Loxopterygium (Anacardiaceae), which display a similar disjunct distribution pattern in this forest type, have different species in these isolated pockets of dry vegetation. It was suspected that some of the taxonomic confusion in the G. spinosa–G. striata complex might be explained by morphological variation between the disjunct areas of its distribution. However, this taxonomic revision shows that geographical isolation does not appear to have caused any significant morphological diversification of the G. spinosa–G. striata complex, and the variation appears more likely to be ecotypic. Therefore, only a single species, Geoffroea spinosa, should be recognized.

Hooker and Arnott, in Hooker (1833), published the genus Gourliea, typified by Gourliea decorticans, based on some spiny plants collected by the Scottish botanist Gillies in Argentina. It was not until 1949 that Burkart formally recognized the similarities of this species with Geoffroea and published the combination Geoffroea decorticans (Gillies ex Hook. & Arn.) Burkart. Geoffroea decorticans displays much morphological variation and although varieties have been recognized within it, this revision does not maintain them because they are based upon weak and inconsistent characters.

Geoffroya L., in Murray, Syst. Veg. ed. 13: 556 (1774) orth. var.
Type: Geoffroea spinosa Jacq.
Type: G. decorticans Gillies ex Hook. & Arn.

Trees or shrubs; DBH 6–60cm. Spines often present on branches and twigs, in the axils of the leaves and at the tips of the twigs; the youngest twigs pubescent, becoming glabrous. Stipules present and caducous, or present in seedlings only. Leaves in groups of 1–5, growing from the same point or from short brachyblasts, imparipinnate; rachis grooved or channelled above; leaflets 5–27, subopposite, oblong-elliptic
or obovate to narrowly so, smaller towards the base of the leaf, the terminal leaflet
either larger or smaller than the lateral leaflets. *Racemes* axillary, erect. *Bracts* caducous. *Bracteoles* occasionally present, attached c.0.5–1mm from the base of the calyx, caducous. *Buds* erect. *Flowers* pedicellate. *Calyx* 5-lobed, imbricate in bud, teeth triangular, subequal, or the upper two almost fused with a shallow notch between them, sometimes with glandular hairs. *Corolla* with five free petals, dark yellow with red veins; keel petals imbricate along the lower edge, as long as or slightly shorter than the wings; stamens 10, fused up to half way or less, vexillary stamen free; anthers dorsifixed, splitting longitudinally; gynoecium as long as or shorter than the androecium; ovary sparsely to densely pubescent, with 1–4 ovules. *Fruit* drupaceous, indehiscent, globose, ovoid, or almond-shaped and slightly flattened, densely short velvety pubescent or glabrous, one-seeded. *Seed* dark red.

**Key to the species of Geoffroea**

1a. Leaflets with eight or fewer pairs of secondary veins, sessile or with a petiolule to 1mm long (in mature leaves); fruit glabrous; keel petals slightly shorter than the wings __________ 1. *G. decorticans*

1b. Leaflets with (9–)12 or more pairs of secondary veins, with a petiolule 1–2mm long (in mature leaves); fruit densely velvety pubescent; keel petals as long as the wings __________ 2. *G. spinosa*

1. **Geoffroea decorticans** (Gillies ex Hook. & Arn.) Burkart, Darwiniana 9 (1): 19 (1949). **Fig. 1.**


*Gourliea chilensis* Clos in Gay, Fl. Chil. 2: 218 (1846) nom. illegit. Type: Amériq. Méridle., Chile, Gay s.n. (holo. TL; iso. K!).


FIG 1. Geoffroea spinosa and G. decorticans. Geoffroea spinosa (drawn from Tressens 1035): A, habit; B, leaflet; C, fruit; D, standard; E, wing; F, keel; G, calyx; H, gynoecium; I, stamens. Geoffroea decorticans (drawn from Gardner & Knees 5823): J, habit; K, leaflet; L, fruit; M, standard; N, wing; O, keel; P, calyx. All scale bars 1cm.
Tree or shrub, 2–12m tall; DBH to 60cm. Bark flaking or peeling off in scrolls to show patches of young green inner bark beneath. Branches and twigs often armed with spines, spines 6–53mm; twigs often spine-tipped, the youngest twigs densely to sparsely pubescent. Stipules present in seedlings only, none seen in the mature plant, presumably very early caducous. Leaves with a rachis 5–80mm, channelled above, sparsely and shortly pubescent; petiole 2–21mm; petiolules to 0.5mm or leaflets sessile; leaflets 5–11, oblong-elliptic to narrowly so, the apex rounded or occasionally truncate, the base rounded, 2–29 × 1–13mm, the terminal leaflet generally larger, 3–31 × 2–11mm; shortly pubescent to glabrous above and beneath; veins reticulate, midvein usually prominent beneath. Racemes in groups of 1–7 from short brachyblasts, the inflorescence axis 5–80mm long, shortly pubescent, 4–35-flowered; peduncle 1–19mm. Bracts ovate, cupped, 1–2 × 1mm, densely pubescent. Pedicels very slender, 2–12mm, with short hairs, glabrescent towards the base. Bracteoles occasionally present, c.1mm, filiform to subulate, pubescent. Flowers erect, 6–10mm, usually flowering before the leaves appear, or when they are immature. Calyx 2–5mm, teeth broad, triangular, 0.5–1mm long, pubescent to densely so. Standard orbicular, blade 6–7.5 × 6.5–8mm, claw 1.5–2mm; wing blade 6–8.5 × 3–5.5mm, the claw 2.5–3mm; keel shorter than the wings, blade 4–5.5 × 2–2.5mm, claw 2.5–3mm; stamens fused to 0.5–1.2mm; vexillary stamen shortest, 3–4mm; central stamen longest, 5–6mm; anthers c.0.5mm; gynoecium about as long as the androecium, 5–6mm; style glabrous; ovary sparsely hairy; ovules 4. Fruit ellipsoid to globose, or almond-shaped and slightly flattened, 12–30 × 10–24mm, glabrous. Seed dark red when dry.

Distribution (Fig. 2). Northern half of Chile and Argentina, as far as Rio Negro, west to Buenos Aires and south to Uruguay. Also present in Paraguay and southern Bolivia.

Altitude. 125–2550m.

Flowering. At the end of the dry season; generally August to September with occasional records in July and October–November. The flowering patterns correspond with the ‘big-bang’ species of Gentry (1990), where all individuals of the same species bloom together just for a few days, and the time of flowering depends on longitude with those furthest north flowering first (D. Prado, pers. comm.).

Habitat and ecology. Dry open areas; present in the Gran Chaco vegetation areas from which G. spinosa is absent; often near water. This species tolerates highly alkaline soils (D’Angelo et al., 1987) and is the last tree to disappear from the dried up salt marshes of the western Chaco. It withstands temporary water logging, such as the seasonal flooding in the Chaco (D. Prado pers. comm.). It is a woody weed, with clonal roots forming pure populations or ‘islets’, in which a central bigger tree is surrounded by several concentric rings of progressively younger individuals (Lewis et al., 1990).

Vernacular names. Chañar (Argentina, Chile, Bolivia), Cumbará, Kimori (Bolivia).
Uses. The fruit is edible (Martínez 73, Pearce s.n., Argentina; Vargas & Tapia 1053, Bolivia), and sometimes made into jam (King 235, San Luis, Argentina) or used in flavouring wine (Tweedie s.n., Argentina).

Nomenclatural notes. The species Lucuma spinosa Molina, described in 1782, was placed in synonymy under Gourliea chilensis by Clos (1846). This latter name is illegitimate (according to article 52.1 in the International Code of Botanical Nomenclature; Greuter, 1994), because it involved the transfer of a species with a legitimate name (L. spinosa) to another genus without retaining the specific epithet. No type specimen was cited in the original publication of Lucuma spinosa, and none was located in this study; however, the description is clearly of Geoffroea decorticans. Moussy (1860) made a recombination of L. spinosa in Geoffroea (as Geoffroya spinosa (Molina) M. de Moussy), but because this name had already been used by Jacquin in 1760, it is a later homonym, and therefore also illegitimate. The illegitimacy of these names has not been noted in any previous work on Geoffroea.

The first description of Gourliea decorticans includes text taken from the labels of more than one sheet of the type material collected by Gillies, so it is likely that
Hooker and Arnott (in Hooker, 1833) based their description on more than one of these specimens. The Kew sheet has a letter attached to it which describes the plant in detail, including a description of the habit ‘...sometimes reaches the height of 16–20 feet is covered with rich yellow blossoms about the end of Sept. & early in October’ which appears almost exactly in Hooker and Arnott’s description, and the herbarium sheet has pencil sketches of the flower and fruit which also appear in the publication. However, one of the two specimens from the Glasgow herbarium (now at Edinburgh) was chosen here as the lectotype for several reasons. Firstly, Hooker was working in Glasgow when he published the description in 1833, so it makes more sense to choose a Glasgow specimen. Secondly, the name was published from a Gillies manuscript name; and one of the Glasgow sheets has ‘Gourliea decor ticans nov. genus, Dr Gillies’ written on it in Gillies’ handwriting, whereas the Kew sheet lacks this information. Thirdly, the text – ‘Provinces of Mendoza, San Luis & Cordova’ – is written on the sheet chosen as lectotype and is repeated in Hooker and Arnott’s description. Finally, the lectotype has both flowers, fruits and leaves, which fits Hooker and Arnott’s protologue, whereas the Kew and other Glasgow specimen only have flowers.

*Geoffroea decorticans* var. *subtropicalis* (Lillo) Burkart is not recognized as a distinct variety here. The characters used to define it in the original description (shape of the trunk and the scaliness of the bark) were not considered sufficient to maintain the variety and no other morphological characters in specimens determined as var. *subtropicalis* differed from other material of *G. decorticans*.

Note: This species can easily be distinguished from *G. spinosa* by: its leaflets, which are sessile, or with a petiolule up to 1mm long; its smaller leaflets with eight or less pairs of secondary veins and reticulate venation which is not prominent beneath, except sometimes the midvein; the absence of stipules in the mature plant; the very slender pedicels; and the glabrous fruits. Specimens from Chile generally have longer and narrower leaflets than those from elsewhere. Plants from Argentina have very small, elliptic leaflets and short rachises. Some specimens are armed with spines and have spine-tipped twigs, and others appear to lack them.

*Selected specimens examined:* ARGENTINA. Buenos Aires: Campo La Patrona, 15km W Pedro Luro, Bartlett 19920 (US); 25km SE of Carmen de Patagones, Fabris & Schwabe 4913 (NY); Campana, Hunziker 1649 (K, MO); ‘Buenos Ayres & Entre Rios’, Tweedie s.n. (E-GL, K); Villarino, Villamil & Hermann 2326 (NY). Catamarca: Santa Maria, near Sta. Maria, river banks, 1800m, 22 xi 1949, Araque & Barkley 19Ar283 (K); Dep. Andalgalá, edge of river Villavil, vicinity of the Bolsón de Pipanaco, Cantino 336 (GH); Andalgalá, Jorgensen 959 (MO); Andalgalá, Choya –El Tofo, 1400m, 28 xi 1946, Wall & Sparre 990 (K); Andalgalá, Choya – El Tofo, submont., 400m, 28 xi 1946, Wall & Sparre 992 (K); Santa Maria, NE part of Campo del Arenal, Wall s.n. (A). Chaco: Jorgensen 2119 (MO); Dep. General Güemes, Castelli, Pedersen 13994 (MO, NY). Córdoba: Unquillo, Bruch 1926 (NY); Union Bell Ville, Parque ‘Francisco Tau’, Ferrucci 824 (K, MO); Rio Primero, 17 xi 1877, Hieronymus s.n. (K); Córdoba, 19 ix 1877, Hieronymus s.n. (K); Córdoba, Lorentz s.n. (K); Near Cassaffousth, Rose & Russell 21054 (NY); 6km NW Villa Curra Brochero, 31°55'S 64°15'W,
Solomon 4122 (MO). Entre Rios: Dep. Paraná, Parque Urquiza, Troncoso, Bacigalupo & Guaglianone 2360 (NY). Corrientes: Goya, Curran s.n. (US); Empedrado, El Pollo, 2 leagues E, 24 vii 1945, Ibassola 3152 (K); Campo ‘Dios Gracia’ Dep. Mburucuyá, 7 viii 1951, Pedersen 1143 (K, NY); Campo ‘Dios Gracia’, Estancia ‘Santa Teresa’, Dep. Mburucuyá, 26 xi 1951, Pedersen 1143a (K, MO, NY); Dep. Concepción, Rincón de Luna, Estancia ‘La Alicia Ana’, Pedersen 4620 (NY, MO); Dep. San Luis del Palmar, 10 km SE of San Luis del Palmar, Quarin & Tressens 1370 (K); Dep. Esquina, near Esquina, Schinini & Carnevali 24942 (F). Jujuy: Estes Hacienda, about 40 km N of Jujuy, 1200 m, 5 x 1938, Eyerdam & Beetle 22242 (K, MO); Dep. Palpalá, 11 km along road 9 from El Carmen to Jujuy, 65°14′W 24′17′S, Klitgaard & Lewis 106 (K); Department Capital, dirt tract to Finca La Cruz, off road no.34, 65°15′S 24′49′S, Klitgaard, Lewis & Ahumada 107 (K, NY); Dep. San Pedro, next to river San Pedro, Legname & Cezzio 8590 (GH). La Pampa: Uruburu, Fortuna 21 (NY); Victorica, Wetmore 844 (US). La Rioja: Dep. Gral. Sarmiento, Vinchina, Meyer 4036 (US); Villa Unión, Meyer 4174 (US). Mendoza: Lupín-Cuchilla del Carrizal, Semper 136 (NY); Around St Raphael and Rio Atuel valley, Wilezek 97 (US). Rio Negro: Dep. Avellaneda, Choole Choel, O’Donnell 1832 (NY); Dep. Adolfo Alsina, 40 km NW of Viedma, alt. 30 m, 18 xii 1938, Eyerdam, Beetle & Grondona 23563 (K). Salta: On road 68 from Salta to La Viña (43 km) where road crosses Arroyo Viñaco, Klitgaard, Lewis & Ahumada 109 (K); Rio Juramento, Meyer 14203 (MO); Cerro San Bernardo, Meyer 35764 (NY); 7 km passing Metán (a Galpón), Meyer & Vacca 23290 (GH); Dep. Capital, Rotonda de Limache, Novara 2833 (MO); Dep. Anta, a 65 km of Las Lajitas camino a Rivadavia, Saravia et al. 10366c (F); Dep. La Viña, Talapampa, Vanni 474 (K); Candelaria, Sierra de la Candelaria, alt. 800 m, 12 ix 1929, Venturi 9496 (K, NY, MO). San Juan: San Agustín del Valle Fértil, Bartlett 19549 (US). San Luis: Pedernera, F.C.P., King 235 (NY). Santa Fe: Dep. Vera. 5 km E of Ayo. Golondrinas, road to Fortín Olmos, Cristóbal et al. 2018 (F); Dep. 9 de Julio, Independencia, 23 viii 1987, Krapovickas & Vanni 41899 (A, F, K, MO). Santiago del Estero: Dep. Guasayán, Campo Verde, Bartlett 20413 (US); Dep. Banda, La Banda, Caro, Martinez 73 (NY). Tucumán: Tranca, before Tapia, Cezzio & Legname 5764c (GH); Dep. Leales, Las Encrucijadas, Ousset 68 (GH); Plains of Tucumán, i 1864, Pearce s.n. (K); Tapia, Seigler & Vervoost DS-10106 (MO); Leales, Venturi 477 (US); Venturi 2490 (US).

BOLIVIA. Tarija: Prov. Gran Chaco, 15 km N of Yacuiba, Campo Pajoso, Beck, Michel & Garcia 11503 (NY); Prov. Cercado, Fewer 7539a (NY); Aviles, village of Tojo, between Tupiza and Tarija, 21°45′S 65°25′W, Kileen 2684 (NY); Gran Chaco, 21°10′S 63°35′W, Kileen 2725 (F, MO, NY); Prov. Cercado, Tarija, 18 km before Entre Ríos, Liberman & Beck 9636 (NY). Santa Cruz: Prov. Andrés Ibáñez, Barrio Héroes del Chaco, 17°48′S 63°08′W, Saldías et al. 1187 (NY); Prov. Cordillera, La Brecha, Bárquitos del Izozog, 19°35′S 62°35′W, Vargas & Tapia 1053 (NY). Location uncertain: Prov. Larecaja, Viens Sorveta, San Pedro, alt. 2550 m, 1861, Mandon 148 (K); southern Bolivia. alt. 1000 m, 18 ii 1904, Fiebrig 2719 (K).

CHILE. Atacama: Copiapó, 27°22′S 70°21′W, Arsonon 7731 (K); Atacama, Prov. Huasco, Gardner & Kees 5823 (E); Prov. Atacama, Dep. Copiapó, 2000 m, 4.11.1925, Johnston 4961 (GH, K); Desert of Atacama, ix-x 1890, Morong 1189 (K, MO, NY); Copiapó valley, 27°20′S 70°35′W, Muñoz et al. 2877 (MO); Prov. Atacama, Dep. Copiapó, c. 500 m, ix 1924, Werdermann 411 (K, MO); Prov. Atacama, on the pass of Pajonales, Zöllner 18315 (MO). Coquimbo: Dep. Elqui, Cerros Casablanca, 3 km W along road from Vicuña, Wagnerknecht 18413 (MO); Prov. Coquimbo, on the pass of Pajonales, Zöllner 9255 (MO). Tarapacá: Valle de Azapa, 4–12 km W of Arica, 18°25′S 70°23′W, Arsonon 7770 (K, MO); Bridges 1284 (K). Location uncertain: Amérix. Mérilde., Gay s.n. (K); San Juan and Laibal. Jameson 16 (K); iv 1867, Thomson s.n. (K); Herbarium Chilense ‘Purchased of Mr E.C. Reed, Dec. 1873, 29′30′, Reed s.n. (K).
PARAGUAY. Boquerón: 25km N of Filadelfia, Schinini et al. 20186 (A, F, K). Gran Chaco: Gran Chaco, Pride s.n. (K); Presidente Hayes: Rio Verde, Pozo Colorado, Casas & Molero 4466 (MO, NY); Ruta Mcal Díaz, 23°42'27"S 59°31'24"W, Degen & Merelles 2992 (MO); Estancia ‘La Perla’, Pedersen 14603 (MO); Pilcomayo River, Morong 1024 (MO, NY).


URUGUAY. Paysandu: Paysandu, Ball s.n. (US).

2. Geoffroea spinosa Jacq., Enum. Syst. Pl.: 28 (1760) as ‘Geoffraea spinosa’. Fig. 1.


Tree 3–20m tall, often with a wide crown; DBH to 50cm. Bark with deep vertical fissures, the slash slowly producing abundant red exudate. Older branches and twigs often with axillary spines, spines 2–36mm; young twigs with a dense to sparse tomentum, becoming glabrous on older twigs. Stipules triangular to narrowly so, 2–10 × 0.5–3mm, with a short, dense pubescence, caducous. Leaves with a rachis 33–200mm, grooved or channelled above, sparsely hairy to glabrous; petiole 5–50mm; petiolule 1–2mm, densely to sparsely pubescent or glabrous; leaflets 7–27, obovate to oblong-elliptic or narrowly so, apex rounded to truncate and often notched, base rounded to obtuse, 8–49 × 3–25mm, the terminal leaflet obovate, shorter than the other leaflets, 8–35mm, sparsely pubescent to glabrous above and beneath, less pubescent beneath except on the midvein; lateral veins parallel, the midvein and lateral veins prominent beneath. Racemes in groups of 1–4 growing from the same point in the leaf axils or from short brachylasts, the inflorescence axis 23–200mm, shortly pubescent, 7–60 flowered; peduncle 5–95mm. Bracts cupped, 2–9 × 1–3mm, pubescent. Pedicels 1–9–(14)mm, pubescent to densely so, sometimes with glandular hairs. Bracteoles occasionally present, c.1–2mm, filiform, densely pubescent. Flowers reflexed, 9–15mm. Calyx 4–9mm, with five triangular teeth, 2–3mm, pubescent to densely so, sometimes with glandular hairs. Standard orbicular to elliptic-ovate or narrowly so, blade 6–11 × 5–12mm, claw 2–5mm; wing blade 7–12 × 3–5mm, the claw 4–5mm; keel as long as the wings, blade 6–8 × 3–4mm, claw 4–5mm; stamens fused up to about half their length, vexillary stamen 6–10mm; central stamen longest, 8–14mm, white; anthers c.1mm; gynoecium as long as or much shorter than the androecium, 5–13mm; style sparsely pubescent to glabrous; ovary densely hairy;
ovules 1–3. *Fruit* ellipsoid to ovoid, sometimes with a short 1–3mm stipe, 21–37 (including stipe) × 15–32mm, green when fresh, densely short velvety pubescent; endocarp hard, buff. *Seed* c.20 × 10mm, dark red when dry.

**Distribution (Fig. 3).** Occurs in five disjunct areas of seasonally dry tropical forests:

Area 1: north-eastern Brazil (northern Ceará, Pernambuco and eastern Bahia).
Area 2: north-eastern Argentina (east of Gran Chaco), Paraguay, Bolivia (north-west of Gran Chaco). This area might represent more than one centre of endemism of seasonally dry tropical forest species (Prado & Gibbbs, 1993), but here is treated a single area.
Area 3: Ecuador, northern Peru.
Area 4: Galapagos.
Area 5: Colombia, Venezuela and the Antilles.

**Altitude.** 5–2500m

**Flowering.** Varies among disjunct areas (see Fig. 3): Area 1, November to February with occasional records in May and August; Area 2, September to January; Area 3, January to May with occasional records in June, August and October; Area 4, February to May; Area 5, February to May with occasional records in July, August and December.

**Habitat and ecology.** Seasonally dry tropical forest (deciduous or semideciduous), or dry pasture and thorny scrub, frequently on flooded ground or next to water.

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![FIG. 3. Distribution of *Geoffroea spinosa* (dots).](image-url)
This species is less common than *Geoffroea decorticans*, and grows as single isolated trees.

**Vernacular names.** Mari, Mary, Marizeiro, Mant, Maú, Umaú (Brazil); Mandubi-guaycurú, Maní de los indios, Maní guaycurú (Argentina); Manduvira (Brazil, Argentina and Paraguay); Sexesuk, Nokiyek (Paraguay); Chauchachi, Chauchapi (Bolivia); Almendro (Peru and Ecuador); Flor de Almendra, Palo seco (Ecuador); Silbadero, Silvadero, Coa (Colombia); Jigua, Pasa de Rio Negro, Quigua, Taque, Taeo (Venezuela); Taki-taki, Palu di Taki, Stakki (Antilles).

**Uses.** The wood is used for carpentry and fuel (Burkart, 1943) in construction (Cerón et al., 11699, Ecuador) and furniture making (Hernández et al. 143, Ecuador). The fruit is edible (Aristeguieta & Zabala 7072, Venezuela; Bernardi 20394, Paraguay; Little 6424, Ecuador). Gardner (1849, p.101) reported that fruits of *G. spinosa* were the principal food of the inhabitants of the Ilha de St. Pedro in the São Francisco river (Alagoas, Brazil) when the river was in flood and they were unable to fish.

**Nomenclatural note.** Kunth (in Humboldt et al., 1823) transferred Robinia striata Willd. to Geoffroea under the name Geoffraea bredemeyeri, putting *R. striata* in synonymy. Although the specific epithet *striata* should have been retained, the name is legitimate because *R. striata* is placed under synonymy according to Bonpland's opinion, *‘teste Bonpl.’*. Therefore, Kunth is expressing doubt about the inclusion of this name in synonymy. Burkart (1949) later synonymized *G. bredemeyeri* Kunth under *Geoffroea striata* (Willd.) Morong. Humboldt & Bonpland (1809) published another species name, Geoffroya superba, commenting that it resembles Robinia striata, but looks very much like a Geoffroea. Morong (1892) also placed this in synonymy under *Geoffroea striata*.

Note: Notes on specimen labels indicate that the presence or absence of spines in this species appears to be related to habitat rather than geography, with spiny treelets usually inhabiting dry scrubland or forest, and those without spines often growing next to water courses. The spiny plants also tend to have smaller leaflets. These two ecotypes have previously been treated as separate species, *G. spinosa* Jacq. and *G. striata* (Willd.) Morong respectively, but the characters are not consistent. Burkart's (1949) key separates the two species by: *‘Ramas de mas de un año con espinas axilares. Foliolos de long. 1–2.5cm, arbusto o arbolito, de campos’* (*G. spinosa*; 'twigs of more than one year with axillary spines. Leaflets 1–2.5cm long, shrub or small tree of campo') or *‘Inerme. Foliolos aprox. de 2–4.5cm de long. Arbol a menudo alto, de orillas de ríos.’* (*G. striata*; 'Spineless. Leaflets 2–4.5cm long. Largish tree of river banks'). However, many specimens studied did not fit into either of these categories. For example, the spineless specimen collected by Charpin & Eskuche (20150) has leaflets ranging from 11–39mm in length. Gentry & Cuadros 47397 was collected in dry scrubby forest, but has no spines, and leaflet lengths measure 13–39mm. Arnoldo-Broeders 3920 has spines, but the leaflet lengths measure 20–27mm. Moreover, one specimen from Brazil, Blanchet 2650, cited by Morong as
G. striata, clearly has axillary spines. No flowering or fruiting characters were found to support the separation of these species, and they are therefore united here as one ecotypically variable species. This type of ecotypic pattern is common in South American dry forest species, where there are often forest and gallery forest ecotypes. These have frequently been described as distinct species, but on further study are revealed to be one variable species. Examples are Andira vermifuga (Mart.) Benth. (Leguminosae) (R.T. Pennington, 1994) and Pouteria ramiflora (Mart.) Radl. (Sapotaceae) (T.D. Pennington, 1990).

The morphological differences between the specimens from disjunct areas of distribution (Fig. 3) of G. spinosa found in this study were slight. All the characters compared overlapped between the areas with no evidence of discontinuous variation. Therefore, geographical isolation does not appear to have caused any significant morphological diversification in this species and there is certainly no basis for recognizing different taxa. Although this study was based largely on herbarium specimens, with limited field observations in Ecuador and Peru, this conclusion is supported by other workers who know G. spinosa in the field. For example, Prado & Gibbs (1993) treated the G. spinosa–G. striata complex as a single species in their biogeographic analysis.

Prado & Gibbs (1993) offered a vicariance explanation for the disjunct distribution of G. spinosa and other species with similar distributions (e.g., Amburana cearensis, Celtis pubescens) in the seasonally dry tropical forests of South America. They argued that the co-incident distribution patterns have resulted from separation of wider common historical distributions rather than by dispersal from different areas, concluding that ‘these fragmentary and mostly disjunct distributional patterns are vestiges of a once extensive and largely contiguous seasonal woodland formation’. Because of the lack of information on the dispersal of G. spinosa, it is hard to evaluate long-distance dispersal as an alternative explanation for its distribution. Geoffroea fruits appear adapted for vertebrate dispersal, as are the morphologically similar small drupaceous Andira fruits that are dispersed by bats (R.T. Pennington & de Lima, 1995). In the case of G. spinosa, the fruits do not have the strong scent associated with bat dispersal, and the only observation of feeding (with no evidence of subsequent seed dispersal) on the fruits of G. spinosa is of the Guayaquil Squirrel (Sciurus stramineus) in north-western Peru (C. Diez, pers. comm.). There might be a capability for dispersal over water, given the presence of this species in the Galapagos, which is a volcanic archipelago, but as the fruits are edible, it is possible that it might have been introduced.


ARGENTINA. Chaco: Dep. 1° de Mayo, Antequera – Cevito route, Charpin & Eskuche AC20150 (F, MO, NY, US); Vicinity of Barranqueras, Curran 87 (NY); Jorgensen 2122 (GH, MO); Resistencia, orillas rio Negro, frente a Fontana, Meyer 8610 (A, NY); Resistencia,

**BOLIVIA.** *Beni*: Trinidad, *Krapovickas & Schinini* 34735 (NY); Prov. Cercado, 7km SW of Trinidad, vic. Puerto Almacén, along Rio Ibare, a tributary paralleling Rio Mamoré, 14°52'S 64°57'W, *Nee* 37548 (NY); *Cochabamba*: Cerro de Duraznillo, *Steinbach* 6023 (F); *Santa Cruz*: Curuyuqui, Transect 1, *Gentry & Pena* 75236 (MO); Prov. Chiquitos, Conseción Don Mario, 125km NE San José de Chiquitos, *Mamani et al.* 1378 (MEXU); 12km E of centre of Santa Cruz on road to Cotoca, Prov. Andrés Ibáñez, *Nee* 33718 (NY); Prov. Andrés Ibáñez, J.B. Santa Cruz, *Nee* 39287 (MEXU, MO, NY); Prov. Andrés Ibáñez, 5km SE comunidad Don Lorenzo, 17°49'S 62°50'W, *Nee & Coimbra* 39938 (MO, NY); Prov. Andrés Ibáñez. 4km SW of Rio Grande, plantas de gas, 18°13'S 62°54'W, *Nee et al.* 44640 (NY); Prov. Cercado, Santa Cruz, *Steinbach* 7297 (A, K, MO).


**COLOMBIA.** *Atlántico*: Near Ponedera, *Dugand* 14 (F); Barranquilla Country Club, *Dugand* 42 (G); Bordering the Magdalena river. In ‘El Paraíso’. Also seen in the hills of Arroyo Jubilado, *Dugand* 523 (F); Barranquilla Country Club golf course, *Dugand* 3137 (COL); Between Palmar de Varela and Ponedera, finca ‘El Paraíso’, *Dugand* 4314 (COL, US); Caribbean coast, region of Barranquilla, Ilanada de Juanmina, *Dugand* 6445 (COL, US); Puerto Colombia, km 16–17 of road, *Dugand & Jaramillo* 3244 (COL, US). *Bolivar*: Mun. Magangue, road Ceibal-La Pascuala and Providencia, *Cuadros* 3189 (MO); Mun. Cartagena, Corregimiento Punta Cañoa, Loma Mogollón, *Cuadros* 3259 (MO); Mun. Cartagena, Isla de Tierrabomba, *Cuadros* 4354 (COL); Mun. Cartagena, Isla Barú, 10°08’N 75°42’W, *Cuadros* 4533 (MO); Mun. Cartagena, Sitio ‘El Pozón’, remains of mangrove, *Cuadros & Gentry* 3082 (MO, NY); Volcán de Lodo, Santa Catalina-Galerazamba road, northern tip of Bolivar, 10°45’N 75°15’W, *Gentry & Cuadros* 47397 (MO); Galerazamba, north tip of Bolivar dep., 10°48’N 75°15’W, near sea level, 30 vi 1984, *Gentry & Cuadros* 47419 (COL, K, MO, NY); Mun. San Martín de Loba, alrededores de Pueblo Nuevo y de la Ciénaga del Totumo, 75°15.8’W 10°17.5’N, *Marulanda* 917 (MO); Zambrano, Bongal, *Rodriguez* 0041 (COL); Mun. de Santa Catalina, 1km S of Galerazamba, along road to Loma de Arena, 10°47’N 75°16’W, *Zarucchi & Cuadros* 3848 (MO); Mun. de Cartagena, 6km SW of crossing of Canal del Dique
at Pasacaballos, Isla Barú, 10°14’N 75°37’W, Zarucchi & Cuadros 3926 (MO). Guajira: 7km from Riohacía, Saravia 2852 (COL); 20km from Maicao towards Uribia, Saravia & Johnson 372 (COL).

**ECUADOR. Azuay:** Balao, Eggers 14568 (A). El Oro: Pasture S of the village, Asplund 15710 (NY); Track between Puerto Pitaheya and Arenillas, de Escobar 1245 (NY); Arenillas, 6km S, Little 6704 (K, NY). Esmeraldas: on plain near airport. In valley of Rio Esmeraldas, 6 v 1943, 6m, Little 6424 (K); Rioverde, Little & Dixon 21217 (NY, US). **Galápagos:** Near Black beach, Charles Island, Howell 9351 (GH); Charles (Isla Floreana) island, near Wilmer’s house, black beach, Leveque 82 (US); Charles Island (Isla Floreana), Linsley 101 (GH); Hood Island, Snodgrass & Heller 738 (GH); Charles Island, 27 ii 1906, Stewart 1588 (F, GH, K, NY). **Guayas:** El Progreso, Asplund 15314 (K, NY, US); Hacienda Barcelona 13–14km from Guayaquil-Salinas, Dodson & Pons 13620 (MO); 3km E of Buenos Aires, Holm-Nielson et al. 2557 (F, MO, NY); Bajada, 49km W of Guayaquil on railway towards Salinas, Little 6755 (NY); Isla Puna, path from Puna Nueva to Estero de los Pozos, Madsen 63127 (QCA); Chanduy, Spruce 6379 (E, K, OXF); Ridge N of Santa Elena, 2°13’S 80°49’W, Svenson 11140 (NY). **Loja:** Below San Pedro, Asplund 18124 (F, K, NY); Near Catamayo, Cornejo & Bonifaz 2174 (GUAY); 20km from Cariamanga (SE) towards El Lucero, 4°22’S 79°30’W, 6 vi 1987, Hughes 1019 (FHO, K); Military base just past Zapotipamba and just past Loja University Field station on main road from Cotacachi, R. T. Pennington et al. 659 (E, K, LOJA, QCNE); Between Loja and Portovelo, Rose 23331 (NY, US); Hacienda ‘La Ceiba’, 8km N of Zapotillo, 4°18’5’S 80°14’W, Samariego & Vivar 004 (US); Seco de Playas valley, Catacocha, Solis 7995 (F); Catamayo valley, nr. La Toma (Catamayo), Wiggins 10956 (MO, NY). **Machalilla, Hacienda La Ceiba,** com. Agua Blanca, Cerón 11699 (MO, PROV); Bahía de Caraquez, in front of Isla Corazón, Cornejo 1756 (GUAY); Capeira 21km, Guayaquil to Daules, Dodson & Gentry 12605 (MO); Estero Manta Blanca, Machalilla Nat. Park, S of Agua Blanca, 1°35’S 80°43’W, Gentry & Josse 72727 (MO); Canton Parroquia Machalilla, del centro de San Sebastián, sector Quimices, Hernandez 143 (QCA); 2km N of Motete, 5km N of Puerto Cayo on the track towards Montecristo, 1°16’S 80°42’W, 1 vi 1987, Hughes 1005 (FHO, K); Machalilla, Rio Salaite, towards sitio El Mate, Josse 575 (QCA); Parque Nacional Machalilla, Agua Blanca, towards Cerro Las Goteras, Josse 692 (QCA); 10km N of Machalilla, 01°25’S 80°40’W, Josse & Valencia 767 (K); Montecristo, Sparre 19891 (QCA).

**PARAGUAY. Alto Paraguay:** Benito Ramos Paredes, near Cerro Barrero, Fuerte Olimpo, Bernardi 20394 (MO); Fiebrig 1407 (K); Campo Loro, 60km NE Filadelfía, Schmeda 1168 (NY, US). **Concepción:** Hassler 7519 (A, K, MO, NY). **Presidente Hayes:** F. G. Briguez, bank of Rio Pilcomayo, Arenas 1568 (NY); Pilcomayo river, Morong 888 (E, GH, MO, NY); Pilcomayo, Rojas 82; Cerro Mbatovi, 25°25’S 57°07’W, Soria & Aguayo 2772 (MO). **Boquerón:** Misión Santa Rosa, Arenas 1686 (NY). **Neembucú:** Curupayty, Bernadi 18472 (MO, NY); Parque Nacional Machalilla, Agua Blanca, towards Cerro Las Goteras, Josse 692 (QCA); 10km N of Machalilla, 01°25’S 80°40’W, Josse & Valencia 767 (K); Montecristo, Sparre 19891 (QCA).

**PERU. Amazonas:** Seasonally dry forest above Rio Utcabamba, c.20km upstream from Bagua Grande, R. T. Pennington et al. 759, 760, 775 (E, MOL). **Piura:** Cauchio Piura, Alban 3976 (MO); El Higueron, camino a Ayabaca, Quiroz 2136 (F). **Tumbes:** 5–8km S of Cerro de Amotape, Quebrada Madre, Base of Cerros de Amotape, Gentry & Diaz 58192 (MO); 5–8km S of Cerro de Amotape, Quebrada Madre, Base of Cerros de Amotape, Gentry & Diaz 58198 (MO); Coastal Plain between Tumaz and Zarumilla, Weberbauer 7622 (F); Plain SE of Hacienda La Choza, 28 ii–3 iii 1927, Weberbauer 7719 (F, GH, K, MO, NY).

**VENEZUELA. Aragua:** Maracay, Trujillo 3269 (MO); Estación Experimental ‘Paraima’ Cagua, Lopez 916 (MO). **Apure:** La Garciera, Aristeguieta & Zabala 7072 (F, MO, NY). **Carabobo:** Carretera, Los Guayos-Valencia, Tamayo 4083 (F, MO, NY); Between Los Guayos
and Valencia, Saer d'Heguert 818 (NY); El Portachuelo, Williams 10284 (F). Caracas, Bredemeyer s.n. (Microfiche 13668 E, Photo F, MO, NY, GH). Falcon: Cerro de Santa Ana, Paraguana, 80m alt, Ruiz Terán 636 (MO); E end of Cerro Chichiriviche, Dist. Silva, Steyermark & Manara 110742 (MO, US); NE area of Distrito Petit, 69°16'W 11°05'N, Steyermark & González 113781 (F, MO). Guárico: Area of 'El Sombrero', Aristegieta 5966 (NY, US); Garcitas village, on banks of Rio Apurito, Dist. Infante, 66°32'W 7°49'N, Davidse & González 12098a (MO); Dist. Mellado, Carretera Dos Caminos, El Sombrero, via fundo La Rojera, de Rojas et al. 3874 (NY). Sucre: Cumaná, Funcke s.n. (GH); Península de Araya, Liesner & González 12097 (MO); Península de Araya, Liesner & González 12101 (MO). Trujillo: Area of Cotiza, Delgado 171 (F). Zulia: Bunting & Stoddart 8826 (NY).

EXCLUDED SPECIES


Geoffroya discolor Benth., in Hook., J. Bot. 2: 69 (1840) (= Dussia discolor (Benth.) Ducke).


Geoffrea obtusifolia Stokes, Bot. Mat. Med. 4: 46. nom. illegit. (= Andira surinamensis (Bondt) Splitg. ex Amsh.)


Geoffroya retusa Poir. in Lam., Encycl. viii. p.182. 1808; Poir. in Lam., Tab. Encycl., iii. tab. 604, fig. 2 (1823) (= Andira surinamensis (Bondt) Splitg. ex Amsh.).

Geoffroya spinulosa Mart. in Spix and Mart., Reise Bras. 2. p.788 (1828) (= Andira vermifuga (Mart.) Benth.).


Geoffrea tomentosa Poir., in Lam. Encycl. viii: 182 (1808) Geoffroea (A microfiche of the type specimen resembles Meliaceae or Anacardiaceae).

Geoffroya vermifuga Mart. in Spix and Mart., Reise Bras. 2. p.788 (1828) (= Andira vermifuga (Mart.) Benth.).

Geoffroea violacea Pers. Syn. ii. p.278. (1806) (= Dalbergia sp.? We were unable to locate the type, an Aublet collection from French Guiana, at BM, but the illustration in Aublet (1775) resembles a Dalbergia and is certainly not a Geoffroea).
ACKNOWLEDGEMENTS

We thank Maureen Warwick for the illustration, Robert Mill and Mark Watson for help with nomenclatural issues and Brian Schrire, Colin Pendry, two anonymous referees and especially Darién Prado for comments on drafts of this paper.

REFERENCES


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