

A REVISION OF *GEOFFROEA* (LEGUMINOSAE– PAPILIONOIDEAE)

H. IRELAND* & R. T. PENNINGTON†

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 *Geoffraea*, and subsequent orthographic variants in the literature include *Geoffraea* 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

* Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK. Corresponding author.

† Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK.

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.

Geoffroea Jacq., Enum. Syst. Pl.: 7 (1760).

Geoffraea Jacq., Enum. Syst. Pl.: 28 (1760) *orth. var.*

Geoffroya L., in Murray, Syst. Veg. ed. 13: 556 (1774) *orth. var.*

Geoffrea Stokes, Bot. Mat. Med.: 46 (1812) *orth. var.*

Type: *Geoffroea spinosa* Jacq.

Syn.: *Gourliea* Gillies ex Hook. & Arn., in Hooker, Bot. Misc. 3: 207 (1833).

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.**

Syn.: *Gourliea decorticans* Gillies ex Hook. & Arn., in Hooker, *Bot. Misc.* 3: 208, t.105 (1833).

Lucuma spinosa Molina, *Sag. Stor. Nat. Chile*: 188, 352 (1782). Type: Not known.

Gourliea decorticata Walp., *Repert. Bot. Syst.* 1: 807 (1842) *nom. illegit.* Type: *Walpers* s.n., Chile (holo. Herb. Walp. Location unknown).

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

Geoffroya spinosa (Molina) M. de Moussy, *nom. illegit.* *Descript. Confederat. Argentine* 1: 403 (1860) non Jacq. (1760).

Gourliea spinosa (Molina) Skeels, *Bull. U.S.D.A. Bur. Pl. Industr.* 162: 31 (1909).

Gourliea decorticans var. *subtropicalis* Lillo, in Venturi & Lillo, *Contr. Arb. Argent.*: 43 (1910). Type: Argentina, Prov. Tucumán, Salta, Jujuy, *S. Venturi* 341. (holo. LIL, Xerox!).

Geoffroea decorticans var. *subtropicalis* (Lillo) Burkart, *Darwiniana* 9 (1): 20 (1949).

Type: Argentina, 'Provinces of Mendoza, San Luis and Cordova', *L. Gillies* s.n. (lecto. E-GL!, designated here; isolectos. E-GL! K! BM!).

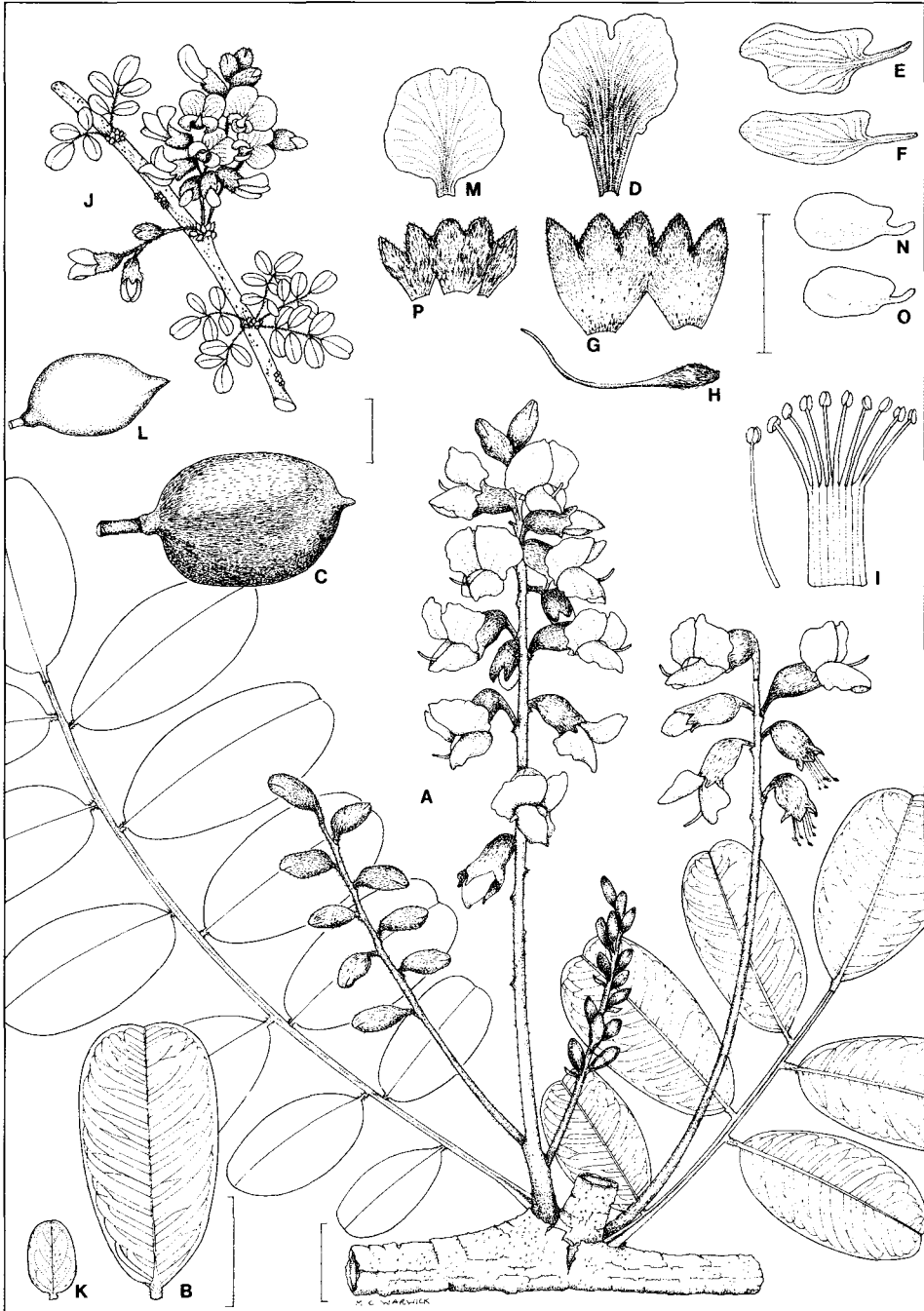


FIG 1. *Geoffroea spinosa* and *G. decorticans*. *Geoffroea spinosa* (drawn from Tressens 1035): A, habit; B, leaflet; C, fruit; D, standard; E, wing; F, keel; G, calyx; H, gynoeceum; I, stamens. *Geoffroea decorticans* (drawn from Gardner & Knees 5823): J, habit; K, leaflet; L, fruit; M, standard; N, 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).

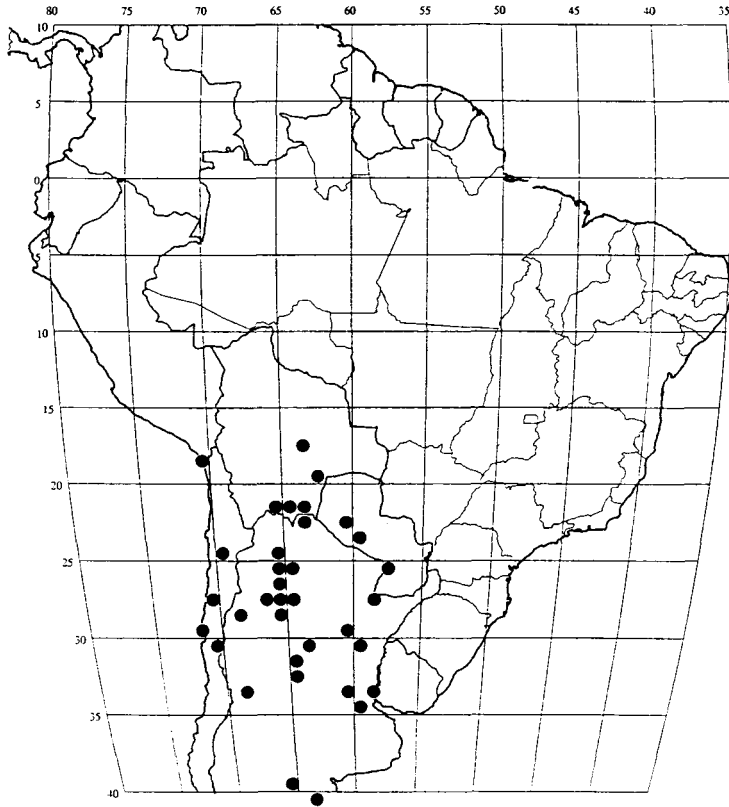


FIG. 2. Distribution of *Geoffroea decorticans* (dots).

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 decorticans* 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 María, near Sta. María, 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, Jørgensen 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 María, NE part of Campo del Arenal, Wall s.n. (A). Chaco: Jørgensen 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); Río 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 Cura Brochero, 31°55’S 64°15’W,

Solomon 4122 (MO). *Entre Ríos*: Dep. Paraná, Parque Urquiza, *Troncoso, Bacigalupo & Guaglianone* 2360 (NY). *Corrientes*: Goya, *Curran s.n.* (US); Empedrado, El Pollo, 2 leagues E, 24 viii 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, 10km SE of San Luis del Palmar, *Quarín & Tressens* 1370 (K); Dep. Esquina, near Esquina, *Schinini & Carnevali* 24942 (F). *Jujuy*: Estes Hacienda, about 40km N of Jujuy, 1200m, 5 x 1938, *Eyerdam & Beetle* 22422 (K, MO); Dep. Palpala, 11km 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'N 24°49'S, *Klitgaard, Lewis & Ahumada* 107 (K, NY); Dep. San Pedro, next to river San Pedro, *Legname & Cuezco* 8590 (GH). *La Pampa*: Uriburu, *Fortuna* 21 (NY); Victorica, *Wetmore* 844 (US). *La Rioja*, Dep. Gral. Sarmiento, Vinchina, *Meyer* 4036 (US); Villa Unión, *Meyer* 4174 (US). *Mendoza* Luján-Cuchilla del Carrizal, *Semper* 121 (NY); Luján-Cuchilla del Carrizal, *Semper* 136 (NY); Around St Raphael and Rio Atuel valley, *Wilczek* 97 (US). *Río Negro*: Dep. Avellaneda, Choel Choel, *O'Donnell* 1832 (NY); Dep. Adolfo Alsina, 40km NW of Viedma, alt. 30m, 18 xii 1938, *Eyerdam, Beetle & Grondona* 23563 (K). *Salta*: On road 68 from Salta to La Viña (43km) where road crosses Arroyo Viñaco, *Klitgaard, Lewis & Ahumada* 109 (K); Río Juramento, *Meyer* 14203 (MO); Cerro San Bernardo, *Meyer* 35764 (NY); 7km pasando Metán (a Galpón), *Meyer & Vaca* 23290 (GH); Dep. Capital, Rotonda de Limache, *Novara* 2833 (MO); Dep. Anta, a 65km de Las Lajitas camino a Rivadavia, *Saravia et al.* 10366c (F); Dep. La Viña, Talapampa, *Vanni* 474 (K); Candelaria, Sierra de la Candelaria, alt. 800m, 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. 5km 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, Camino a Antaje, *Ferrucci et al.* 606 (F, K); Dep. Banda, La Banda, *Martínez* 73 (NY). *Tucumán*: Trancas, before Tapia, *Cuezco & Legname* 5764c (GH); Dep. Leales, Las Encrucijadas, *Ousset* 68 (GH); Plains of Tucumán, i 1864, *Pearce s.n.* (K); Tapia, *Seigler & Vervoort* DS-10106 (MO); Leales, *Venturi* 477 (US); *Venturi* 2490 (US).

BOLIVIA. *Tarija*: Prov. Gran Chaco, 15km N of Yacuiba, Campo Pajoso, *Beck, Michel & García* 11503 (NY); Prov. Cercado, *Feuerer* 7539a (NY); Aviles, village of Tojo, between Tupiza and Tarija, 21°45'S 65°25'W, *Killeen* 2684 (NY); Gran Chaco, 21°10'S 63°35'W, *Killeen* 2725 (F, MO, NY); Prov. Cercado, Tarija, 18km 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, Bañados del Izozog, 19°35'S 62°35'W, *Vargas & Tapia* 1053 (NY). *Location uncertain*: Prov. Larecaja, Vienst Sorveta, San Pedro, alt. 2550m, 1861, *Mandon* 148 (K); southern Bolivia. alt. 1000m, 18 ii 1904, *Fiebrig* 2719 (K).

CHILE. *Atacama*: Copiapó, 27°22'S 70°21'W, *Aronson* 7731 (K); Atacama, Prov. Huasco, *Gardner & Knees* 5823 (E); Prov. Atacama, Dep. Copiapó, 2000m, 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.500m, ix 1924, *Werdermann* 411 (K, MO); Prov. Atacama, on the pass of Pajonales, *Zöllner* 18315 (MO). *Coquimbo*: Dep. Elqui, Cerros Casablanca, 3km W along road from Vicuña, *Wagenknecht* 18413 (MO); Prov. Coquimbo, on the pass of Pajonales, *Zöllner* 9255 (MO). *Tarapacá*: Valle de Azapa, 4-12km W of Arica, 18°25'S 70°23'W, *Aronson* 7770 (K, MO); *Bridges* 1284 (K). *Location uncertain*: Amériq. Méridle., *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.* 21086 (A, F, K). *Gran Chaco*: Gran Chaco, *Pride s.n.* (K); *Presidente Hayes*: Río Verde, Pozo Colorado, *Casas & Molero* 4466 (MO, NY); *Ruta Mcal Díaz*, 23°42'27"S 59°31'24"W, *Degen & Mereles* 2992 (MO); Estancia 'La Perla', *Pedersen* 14603 (MO); *Pilcomayo River*, *Morong* 1024 (MO, NY).

PERU/CHILE (uncertain). *Tacna?*: *Cobija*, *Iquiqui* and *Arica*, 1831, *Cumming* 921 (K).

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

2. *Geoffroea spinosa* Jacq., *Enum. Syst. Pl.*: 28 (1760) as '*Geoffraea spinosa*'. **Fig. 1.** Syn.: *Robinia striata* Willd., *Sp. Pl.* 3(2): 1132 (1803). Type: Venezuela, Caracas, *W. Bredemeyer s.n.* (holo. B-Willd. Microfiche 13668: E!, photo. F! MO! NY! GH!).

Geoffroya superba Humb. & Bonpl., *Pl. Æquinoc. 2*: 69 (1809). Type: Ecuador, *Tomependa*, *Humboldt* 3607. (holo. P. microfiche 160/18. K!; iso. F!).

Geoffraea bredermeyer Kunth. in Humb., *Bonpl. & Kunth*, *Nov. Gen. Sp.* 6: 370 (1823). Type: Venezuela, *Prov. Aragua*, *Humboldt* 756. (holo. P. Microfiche 160/20. K!).

Geoffroea striata (Willd.) *Morong*, *Ann. New York Acad. Sci.* 7: 87 (1892).

Geoffroea striata (Willd.) J.F. Macbr., *Publ. Field Mus. Nat. Hist., Bot. Ser.* 8 (2): 102 (1930) *nom. illegit.*

Type: [icon] *Piso, W. & Marcgrave, G.* (1648) *Historia Naturalis Brasilia*. Leiden and Amsterdam; 120, Lib. 3, Cap. 13, 'Umari'.

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 brachyblasts, 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-obovate 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; gynoeccium as long as or much shorter than the androeccium, 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 & Gibbs, 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.

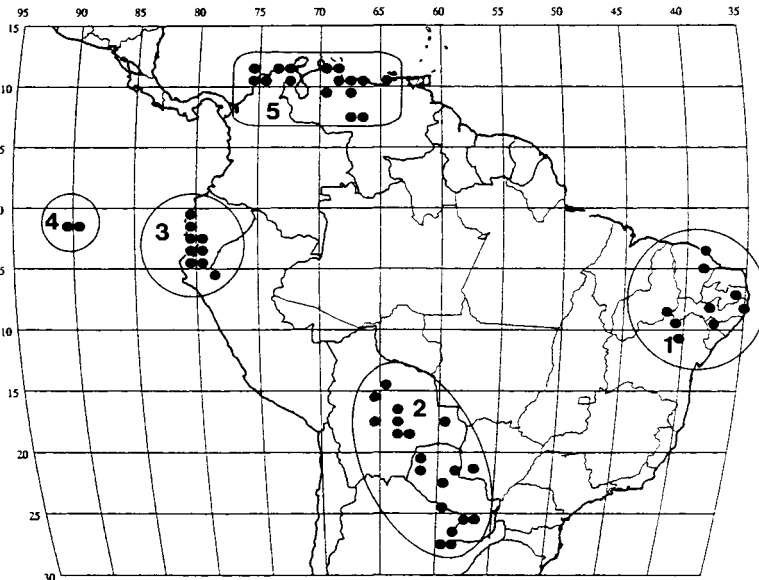


FIG. 3. Distribution of *Geoffroea spinosa* (dots).

This species is less common than *Geoffroea decorticans*, and grows as single isolated trees.

Vernacular names. Mari, Mary, Marizeiro, Mant, Maú, Umari, 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 Río Negro, Quigua, Taque, Tao (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 más de un año con espinas axilares. Foliólos 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. Foliólos aprox. de 2–4.5cm de long. Árbol 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.

Selected specimens examined: ANTILLES. Curaçao: Levengebergte, *Arnoldo-Broeders* 2115 (US); Knip, *Arnoldo-Broeders* 3920 (A, NY, US); *Curran & Hamman* 223 (NY). Bonaire: *Boldingh* 7141 (NY); *Curran & Hamman* 89 (GH, NY). Aruba: Balushi district, *Howard* 20288 (A, NY).

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

barranca riacho Negro, *Rojas* 11554 (CHI); Dep. 1° de Mayo, Pto. Antequera, alt. 10–15m, 25.4.1985, *Schinini, Niklas & Vodicka* 24328 (F, K). *Corrientes*: Estancia ‘Las Tres Marias’ by Rio Paraná, Dep. Empedrado, *Pederson* 7499 (E, K); Dep. San Luis del Palmar, Riachuelito, *Rumiz* 158 (MEXU); Dep. San Cosme, Paso de la Patria, banks of río Paraná, *Tressens* 1035 (F, K, MEXU). *Formosa*: Río Coltapick Estancia ‘Herradura’, Dep. Boca del Bermejo, *Pedersen* 1261 (US); Dep. Bermejo, Río Paraná, Isla del Cerrito, *Schinini* 27635 (GH, MO).

BOLIVIA. *Beni*: Trinidad, *Krapovickas & Schinini* 34735 (NY); Prov. Cercado, 7km SW of Trinidad, vic. Puerto Almacén, along Río Ibare, a tributary paralleling Río 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 Río Grande, plantas de gas, 18°13'S 62°54'W, *Nee et al.* 44640 (NY); Prov. Cercado, Santa Cruz, *Steinbach* 7297 (A, K, MO).

BRAZIL. *Bahia*: Serra Jacobina, Bahia, 1837, *Blanchet* 2650 (E, F, K, NY, OXF, RB); Municipio de Barra, Bahia Lagoa Juazinho, *Elias de Paula* 3160 (UB); Curaca, *Interaminense s.n.* (IPA); Route Itagimirim/ Salto da Divisa Pastaria, *Pinheiro* 1721 (US). *Ceará*: Río Maranguapinho, Bano Vermelho, Mun. de Fortaleza, *Drouet* 2703 (F, GH); Wooded bottoms of Pacotyat Fortaleza, Recife road, Mun. de Pacatuba, *Drouet* 2718 (F, GH, NY, US); Quixadá, 14 iv 1909, *Ducke* 2158 (RB); Fortaleza, low ground on road from Maranguape, 1 xii 1955, *Ducke* 2504 (K, RB); *Gardner* 1911 (E, K, MO, NY, OXF); Sequeira, *Lima* 12/67 (IPA). *Mato Grosso do Sul*: Porto Murtinho, Hotel dos Camalotes, *Pott et al.* 4620 (K). *Paraíba*: Itabaina, Sítio Canto Alegre, near rio Paraíba, *Acad. Bras. de Ciencias* 1016/21346 (IPA). *Pernambuco*: Near Rio São Francisco, c.7km from Petrolina, *Carauta* 1005 (RB); Iputinga-Recife-Pernambuco, *Difens* 636 (RB); Bank of Rio São Francisco, 5km Norte CPATSA, Setor Sementes, *Fotius* 3598 (IPA); *Gardner* 964 (E, GH, K, NY, OXF); Inajá, 29 v 1971, *Heringer et al.* 979 (IPA, RB); Recife, suburb, *Lima s.n.* (US); São Jose do Belmonte, Bom Nome, after village in direction of Serra Talhada, *Pereira et al.* 756 (IPA); Victoria, *Pickel* 1860 (IPA); Recife-Iputinga. Zone between forest and beach, *Sobrinho s.n.* (RB).

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). *Bolívar*: Mun. Magangue, road Ceibal-La Pascuala and Providencia, *Cuadros* 3189 (MO); Mun. Cartagena, Corregimiento Punta Canoa, 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, Sítio ‘El Pozón’, remains of mangrove, *Cuadros & Gentry* 3082 (MO, NY); Volcán de Lodo, Santa Catalina-Galerazamba road, northern tip of Bolívar, 10°45'N 75°15'W, *Gentry & Cuadros* 47397 (MO); Galerazamba, north tip of Bolívar 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 Riohacia, *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 Pitahaya 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 Cotacacha, *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'S 80°14'W, *Samaniego & Vivar* 004 (US); Seco de Playas valley, Catacocha, *Solis* 7995 (F); Catamayo valley, nr. La Toma (Catamayo), *Wiggins* 10956 (MO, NY). *Manabi*, Jipijapa Cantón Parroquia Machalilla, 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 Jipijapa, Parroquia Machalilla, del centro de San Sebastián, sector Quimices, *Hernández* 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 Filadelfia, *Schmeda* 1168 (NY, US). *Concepción*: *Hassler* 7519 (A, K, MO, NY). *Presidente Hayes*: Fn. Gral. Bruguez, bank of Rio Pilcomayo, *Arenas* 1568 (NY); Pilcomayo river, *Morong* 888 (E, GH, MO, NY); Pilcomayo, *Rojas* 82; Cerro Mbatoví, 25°25'S 57°07'W, *Soria & Aguayo* 2772 (MO). *Boquerón*: Misión Santa Rosa, *Arenas* 1686 (NY). *Neembucú*: Curupayty, Humaitá, *Bernadi* 18472 (MO, NY); opposite the mouth of río Bermejo, Dep. Pilar, *Meyer* 16123 (E);

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 Higuerón, camino a Ayabaca, *Quiroz* 2136 (F). *Tumbes*: 5–8km S of Cherrelieque zona 'Peña Blanca', Quebrada Madre, Base of Cerros de Amotape, *Gentry & Diaz* 58192 (MO); 5–8km S of Cherrelieque zona 'Peña Blanca', 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). *Falcón*: Cerro de Santa Ana, Paraguaná, 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', *Aristeguieta* 5966 (NY, US); Garcitas village, on banks of Río Apurito, Dist. Infante, 66°32'W 7°49'N, *Davidse & González* 12098a (MO); Dist. Mellado, Carretera Dos Caminos, El Sombrero, vía 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

- Geoffrea acutifolia* Stokes, Bot. Mat. Med. 4: 46. nom. illegit. (= *Andira inermis* (W. Wright) DC. subsp. *inermis*).
- Geoffroya discolor* Benth., in Hook., J. Bot. 2: 69 (1840) (= *Dussia discolor* (Benth.) Amsh.).
- Geoffroya goyazensis* Glaz., in Bull. Soc. Bot. France. lii Mem. iii: 151 (1906) (= *Vatairea macrocarpa* (Benth.) Ducke).
- Geoffraea inermis* W. Wright, Lond. Med. J.: 256–257 (1787) (= *Andira inermis* (W. Wright) DC. subsp. *inermis*).
- Geoffraea inermis jamaicensis* W. Wright, Philos. Trans. 67: 507–512 (1777). nom. illegit. (= *Andira inermis* (W. Wright) DC. subsp. *inermis*).
- Geoffrea obtusifolia* Stokes, Bot. Mat. Med. 4: 46. nom. illegit. (= *Andira surinamensis* (Bondt) Splitg. ex Amsh.)
- Geoffroya pubescens* Rich. in Actes Soc. Hist. Nat. Paris. 1(1): 111 (1792) (= *Andira surinamensis* (Bondt) Splitg. ex Amsh.).
- Geoffraea racemosa* Poir., in Lam. Encycl. viii: 183 (1808). nom. illegit. (= *Vouacapoua americana* Aublet).
- 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.).
- Geoffroya surinamensis* Bondt, Dissertatio Medica Inauguralis de Cortice Geoffraeae Surinamensis. pp.8–13, figs 1–8 (1788) (= *Andira surinamensis* (Bondt) Splitg. ex Amshoff).
- Geoffraea 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

- AUBLET, F. (1775). *Hist. Pl. Guiane* iii, t. 301. Paris: P. F. Didot Jeune.
- BENTHAM, G. (1837). *Commentationes de Leguminosarum Generibus*, pp. 43–45. Vindobonae (Vienna): J. P. Sollingeri.
- BENTHAM, G. (1839). De leguminosarum generibus commentationes. *Ann. Mus. Wiener Naturgesch.* 2 (1): 107–109.
- BONDT, N. (1788). *Dissertatio Medica Inauguralis de Cortice Geoffraeae Surinamensis*. Leiden: Lugduni Batavorum.
- BURKART, A. (1949). La posición sistemática del ‘chañar’ y las especies del género *Geoffroea* (Leguminosae–Dalbergieae). *Darwiniana* 9: 9–23.
- CLOS, D. (1846). In: GAY, C. (ed.) *Fl. Chil.* 2: 218. Paris: Fain y Thunot.
- D’ANGELO, C., PRADO, D. E., STOFELLA, S. L. & LEWIS, J. P. (1987). The subchaquenian vegetation of the province of Santa Fe (Argentina). *Phytocoenologia* 15: 329–352.
- FARR, E. R., LEUSSINK, J. A. & STAFLEU, F. A. (1979). *Index Nominum Genericorum (Plantarum)*, vol. 2. Utrecht: Bohn, Scheltema & Holkema.
- GARDNER, G. (1849). *Travels in the Interior of Brazil*. 2nd edition. London: Reeve, Banham & Reeve.
- GENTRY, A. H. (1990). Evolutionary patterns in Neotropical Bignoniaceae. *Mem. New York Bot. Gard.* 55: 118–129.
- GREUTER, W. (ed.) (1994). *International Code of Botanical Nomenclature (Tokyo Code)*. Königstein, Germany: Koeltz Scientific Books.
- HOOKER, W. J. (1833) *Bot. Misc.* 3: 207. London: John Murray.
- HUMBOLDT, A. & BONPLAND, A. J. (1809). *Pl. Aequinoct.* 2: 69.
- HUMBOLDT, A., BONPLAND, A. J. & KUNTH, K. S. (1823). *Nov. Gen. Sp.* 6: 370. Paris: Lutetiae Parisiorum.
- JACQUIN, N. J. (1760). *Enum. Syst. Pl.*: 7, 28. Leiden: Lugduni Batavorum.
- JACQUIN, N. J. (1763). *Select. Stirp. Amer. Hist.*: 207. CLXXX, f. 62. Vindobonae (Vienna): Ex Officina Krausiana.
- LEWIS, J. P., STOFELLA, S. L., PRADO, D. E., PIRE, E. F., FRANCESCHI, E. A. & CARNEVALE, N. J. (1990) Dynamics and development of floristic richness in the vegetation of a large depressed area of the Great Chaco. *Flora* 184: 63–77.
- LINNAEUS, C. (1763). *Sp. Pl.* ed. 2 (2): 1043. Holmiae, Impensis Direct. Laurentii Salvii.
- LINNAEUS, C. (1774). In: MURRAY, J. A. (ed.) *Syst. Veg.* ed. 13: 556. Gottingae et Gothae: Typis et impensis Jo. Christ. Dieterich.
- MOLINA, G. I. (1782). *Sag. Stor. Nat. Chili*: 188, 352. Bologna: C. Guiseppa Grotti.
- MORONG, T. (1892). An enumeration of the plants collected by Dr Thomas Morong in Paraguay 1888–1890. *Ann. New York Acad. Sci.* 7: 87.
- MOUSSY, M. DE (1860). *Description Géographique et Statistique de la Confédération Argentine* 1: 403. Paris: Firmin Didot Frères, fils et cie.

- PENNINGTON, R. T. (1994). *The Taxonomy and Molecular Systematics of Andira*. D.Phil. thesis. Oxford: University of Oxford.
- PENNINGTON, R. T. & DE LIMA H. C. (1995). Two new species of *Andira* from Brazil and the influence of dispersal in determining their distributions. *Kew Bull.* 50: 557–566.
- PENNINGTON, T. D. (1990). *Flora Neotropica. Monograph 52: Sapotaceae*: 279–282. New York: New York Botanical Garden.
- PISO, W. & MARCGRAVE, G. (1648) *Historia Naturalis Brasilia*. Leiden and Amsterdam: L. & D. Elzevirios.
- PRADO, D. E. & GIBBS, P. E. (1993). Patterns of species distributions in the dry seasonal forests of South America. *Ann. Missouri Bot. Gard.* 80: 902–927.
- SPRENGEL, K. P. J. (1818). *Anleit. Kenntn. Gew.* ed. 2 (2): 773.
- STOKES, J. (1812) *Bot. Mat. Med.*: 46. London: J. Johnson & Co.
- WIGGIN, I. L. & PORTER, D. M. (1971). *Flora of the Galapagos Islands*: 621–623. Stanford, California: Stanford University Press.
- WILLDENOW, C. W. (1803). *Sp. Pl.* 3 (2): 1132. Berolini (Berlin): G. C. Nauk.
- WRIGHT, W. W. (1777). Description and use of the cabbage-bark tree of Jamaica. *Philos. Trans.* 67: 507–512.

Received 17 December 1998; accepted with revision 24 February 1999

LIST OF EXSICCATAE

- | | |
|--|--|
| Acad. Bras. de Ciencias, 1016 (2) | Cristobal C.L. <i>et al.</i> , 2018 (1) |
| Alban J., 3976 (2) | Cuadros H., 3189, 3259, 4354, 4533 (2) |
| Arenas P., 1568, 1686 (2) | Cuadros H. & A.H. Gentry, 3082 (2) |
| Aristeguieta L., 5966 (2) | Cumana L.J., 103 (2) |
| Aristeguieta L. & H. Zabala, 7072 (2) | Cumming, 921 (1) |
| Arnoldo-Broeders M., 2115, 3920 (2) | Cuozzo A.R. & P.R. Legname, 5764c (1) |
| Aronson J., 7731, 7770 (1) | Curran H.M., 87 (2); sn (1); 221 (2) |
| Asplund E., 15314, 15710, 18124 (2) | Curran H.M. & M. Haman, 89, 223 (2) |
| Ball J., sn (1) | Davidse G. & A.C. Gonzales, 12098A (2) |
| Bartlett H.H., 19549, 19920, 20413 (1) | de Escobar L.A., 1245 (2) |
| Beck S.G. <i>et al.</i> , 11503 (1) | de Rojas C. <i>et al.</i> , 3874 (2) |
| Bernardi L., 18472, 20394 (2) | Degen, R. & F. Mereles, 2992 (1) |
| Blanchet, 2650 (2) | Delgado E., 171 (2) |
| Boldingh I., 7141 (2) | Difens, 636 (2) |
| Borsini O., 1101 (1) | Dodson C.H. & A.H. Gentry, 12605 (2) |
| Bredemeyer, sn (2) | Dodson C.H. <i>et al.</i> , 13620 (2) |
| Bridges, 1384 (1) | Donell C.A.O., 1832 (1) |
| Bruch C., 1926 (1) | Drouet F., 2703, 2718 (2) |
| Bunting G.S. & A. Stoddart, 8826 (2) | Ducke A., 2158, 2504 (2) |
| Cabrera A.L., 34099 (1) | Dugand A., 14, 42, 523, 1030, 3137, 4314, 6445, s.n. (2) |
| Cantino P., 336 (1) | Dugand A. & R. Jaramillo, 3244 (2) |
| Carauta, 1005 (2) | Duque J.G., (2) |
| Casas, F. & J. Molero, 4466 (1) | Eggers, 14568, 15776 (2) |
| Cerón C. <i>et al.</i> , 11699 (2) | Elias de Paula J., 3106 (2) |
| Charpin A. & U. Eskuche, AC20150 (2) | Eyerdam W.J. & A.A. Beetle, 22422 (1) |
| Cornejo X., 1756 (2) | Eyerdam W.J. <i>et al.</i> , 23563 (1) |
| Cornejo X. & C. Bonifaz, 2174 (2) | |

- Fabris H.A. & H. Schwabe, 4913 (1)
 Ferrucci S., 824 (1)
 Ferrucci S. *et al.*, 606 (1)
 Feuerer, 7539a (1)
 Fiebrig K., 1407 (2); 2719 (1)
 Fortuna J., 21 (1)
 Fotius, 3598 (2)
 Funcke, sn (2)
 Funcke & Siklim, 612 (2)
 Garcia Barriga H., 06414 (2)
 Gardner G., 964, 1415, 1911 (2)
 Gardner M.F. & S.G. Knees, 5823 (1)
 Gay M.C., sn (1)
 Gentry A. & C. Diaz, 58192, 58198 (2)
 Gentry A. & C. Josse, 72727 (2)
 Gentry A. & H. Cuadros, 47397, 47419 (2)
 Gentry A. & M. Pena, 75236 (2)
 Gillies, sn (1)
 Hassler E., 2744, 7519 (2)
 Haught O., 3053 (2)
 Heringer E.P. *et al.*, 979 (2)
 Hernández C. *et al.*, 143 (2)
 Hieronymus G., sn, sn (1)
 Holm-Nielsen *et al.*, 2557 (2)
 Howard R.A., 20288 (2)
 Howell J.T., 9351 (2)
 Hughes C.E., 1005, 1019 (2)
 Hunziker A.T., 22322 (1)
 Hunziker J.H., 1649 (1)
 Ibassola, 3152 (1)
 Interaminense L., sn (2)
 Jaccobs, 16 (1)
 Johnston, 4961 (1)
 Jørgensen P., 2119 (1); 2122 (2)
 Jørgenson, 959 (1)
 Josse C., 575, 692 (2)
 Josse C. & S. Valencia, 767 (2)
 Killeen T., 2684, 2725 (1)
 King D.O., 235 (1)
 Klitgaard B.B. & G.P. Lewis, 106 (1)
 Klitgaard B.B. *et al.*, 107, 109 (1)
 Krapovickas & Vanni, 41899 (1)
 Krapovickas A. & A. Schinini, 34735 (2)
 Kuntze O., sn (1)
 Legname P.R. & A.R. Cuczzo, 8590 (1)
 Liberman & Beck S.G., 9636 (1)
 Liesner R. & A. González, 12097, 12101 (2)
 Lillo, 19Ar283 (1)
 Lima A., 12/67 (2)
 Lima D.A., sn (2)
 Linsley E., 101 (2)
 Little E.L., 6424, 6704, 6755 (2)
 Little E.L. & R.G. Dixon, 21217 (2)
 Lopez F.F., 916 (2)
 Lorentz & Grisebach, sn (1)
 Luis Mille S.J., 994 (2)
 Lèveque R., 82 (2)
 Madsen J.E., 63127 (2)
 Maldouado, 417 (1)
 Mamari F. *et al.*, 1378 (2)
 Mandon, 148 (1)
 Martínez V., 73 (1)
 Marulanda O., 917 (2)
 Meyer T., 4036, 4174 (1); 8610 (2); 14203 (1); 16123 (2); 35764 (1)
 Meyer T. & A.A. Vaca, 23290 (1)
 Morong T., 888 (2); 1024, 1189 (1)
 Muñoz M. *et al.*, 2877 (1)
 Nee M., 33718, 37548, 39287, 46718, 46732 (2)
 Nee M. & G. Coimbra, 39938 (2)
 Nee M. *et al.*, 44640 (2)
 Novara L., 2833 (1)
 Ousset, 68 (1)
 Pearce R., sn (1)
 Pedersen T.M., 1143 (1); 1261 (2); 4620 (1); 7499 (2); 1143a, 13994, 14603 (1)
 Pennington R.T. *et al.*, 659, 759, 760, 775 (2)
 Pereira R. *et al.*, 756 (2)
 Pickel B., 1860 (2)
 Pinheiro R.S., 1721 (2)
 Pires & Furtado, 17339 (2)
 Pittier H., 7941 (2)
 Pott A. *et al.*, 4620 (2)
 Pride A., sn (2)
 Pride A., sn (1)
 Quarín C. & S.G. Tressens, 1370 (1)
 Quiroz L.S., 2136 (2)
 Rodriguez D., 1473 (1)
 Rodriguez M., 0041 (2)
 Rojas, 1658, 11554 (2)
 Rojas T., 82 (2)
 Rose J.N. & P.G. Russell, 21054 (1)
 Rose J.N. *et al.*, 23331 (2)
 Ruiz Terán L., 636 (2)
 Rumiz D.I., 158 (2)
 Saer d'Heguert J., 818 (2)

-
- Saldias M. *et al.*, 1187 (1)
Samaniego A. & F. Vivar, 004 (2)
Saravia C., 2852 (2)
Saravia C. & D. Johnson, 372 (2)
Saravia C.J. *et al.*, 10366c (1)
Schinini A., 27635 (2)
Schinini A. & R. Carnevalli, 24942 (1)
Schinini A. *et al.*, 21086 (1); 24328 (2)
Schmeda G., 1168, 1348 (2)
Semper J., 121, 136 (1)
Siegler D. & F. Verwoorst, DS-10106 (1)
Snodgrass R.E. & E. Heller, 738 (2)
Sobrinho, sn (2)
Solis C.M., 7995 (2)
Solomon J., 4122 (1)
Soria N. & A. Aguayo, 002772 (2)
Sparre B., 19891 (2)
Spruce R., 6379 (2)
Steinbach J., 3125, 6023, 7297 (2)
Stewart A., 1588 (2)
Steyermark J.A. & A. Gonzales, 113781
(2)
Steyermark J.A. & B.J. Manará, 110742
(2)
Svenson H.K., 11140 (2)
Tamayo F., 4083 (2)
Thomson, sn (1)
Tressens S.G., 1035 (2)
Troncoso N.S. *et al.*, 2360 (1)
Trujillo B., 3269 (2)
Tweedie, sn (1)
Vanni R., 474, 824 (1)
Vargas I.G. & S. Ortiz 3217 (2)
Vargas I.G. & E. Tapia, 1053 (1)
Venturi, 9496 (1)
Venturi S., 477, 2490, 9496 (1)
Villamil C.B. & P.M. Herman, 2326, 8103
(1)
Wagenknecht R., 18413 (1)
Wall & Sparre, 990, 992 (1)
Wall E., sn (1)
Weberbauer A., 7622, 7719 (2)
Werdermann E., 411 (1)
Wetmore A., 844 (1)
Wiggins I.L., 10956 (2)
Wilczek, 97 (1)
Wilkes, sn (1)
Williams L., 10284 (2)
Zardini E., 5668 (2)
Zarucchi J.L. & H. Cuadros, 3848, 3926
(2)
Zollner O., 9255, 18315 (1)