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Original Paper

A synopsis of the Caryocaraceae

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Abstract

An update on the taxonomy of the Caryocaraceae is given with descriptions of all 26 species including details of their ecology, uses and distribution. All species are mapped, much further information about the type collections is included and three species are lectotypified.

Key words: *Anthodiscus*, *Caryocar*, Malpighiales, oily fruit, pequi.

Resumo

A sistemática de Caryocaraceae é atualizada com descrições das 26 espécies incluindo ecologia, usos e distribuições com mapas de todas as espécies. São incluídas informações adicionais sobre os tipos. Três espécies são aqui lectotipificadas.

Palavras-chave: Anthodiscus, Caryocar, Malpighiales, fruto oleoso, pequi.

Introduction

The Caryocaraceae is a woody family of 26 species of trees and shrubs that are widely distributed mainly in tropical South America with one species of each genus reaching as for north as Costa Rica. Species of this family have adapted into a wide range of different habitats. The family is important both as source of good timber and for the edible fruits of several species which are used widely as a source of an oil with nutritional and cosmetic value.

Since the monograph of Caryocaraceae (Prance & Silva 1973), two new species have been described, a considerable amount of extra information has been published about the family and many more herbarium collections have been made. This paper is to update the taxonomy and relationships of this small family and to produce more accurate updated maps of the distribution based on the new collections. The 1973 monograph was based on 698 herbarium collections that were available then. The number of specimens has now increased greatly to at least 3,650 studied here, due to the impressive activity of many recent collectors.

Methods

The herbarium collections of several herbaria (BM, CEPEC, COAH, COL, INPA, K, MG, MO, NY, RB) and several databases were reviewed to update the last monograph of Caryocaraceae (Prance & Silva 1973). The locality of type specimens was updated, and barcodes were added where available with the data from Jstor plants and other digitized sources. Lectotypes have been selected for three species. Many more recent collections now exist, and this has amplified the distribution of most species. The specimens are cited according to the geographical arrangement of Brummitt (2001). Recent molecular studies were reviewed, and they place the family firmly in the Malpighiales. At least one specimen from each political division in which a species occurs is cited under the description.

Results and Discussion

Relationships of Caryocaraceae

Syzsyzlowicz (1895) placed the family between Ochnaceae and Marcgraviaceae. Hutchinson (1973) placed the family in his order Theales next to

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the Medusagynaceae. Wettstein (1935) placed Caryocaraceae in his order Guttiferales together with Dilleniaceae, Actinidiaceae, Ochnaceae, Eucryphiaceae, Marcgraviaceae, Theaceae, Guttiferae and Dipterocarpaceae. Cronquist (1968) and Takhtajan (2009) both placed Caryocaraceae in Theales together with Ochnaceae, Marcgraviaceae and Quinaceae and various other small families. Recent molecular studies have placed the family clearly in the Malpighiales, but no close relatives are indicated in the vast sequence analyses from many gene regions of Wurdack & Davis (2009) and Soltis *et al.* (2011). In a 3-gene analysis Soltis *et al.* (2007) recovered a clade, albeit with low support, in which Caryocaraceae + (Linaceae + Irvingiaceae) were sister to Erythroxylaceae + Rhizophoraceae. In Wurdack & Davis (2009) the Caryocaraceae is in a polytomy with Ctenolophonaceae, Humiriaceae, Irvingiaceae, Ixonanthaceae and Linaceae. In a comparative study of the floral structure of these families Matthews & Endress (2011) concluded that a clade of Linaceae, Irvingiaceae and Caryocaraceae is not well supported by floral morphology, and that Caryocaraceae are morphologically the most divergent among these families. Dickinson (1990), in a detailed morphological study of the family, pointed out the similarity of the gynoecium and fruit with the Seychellean endemic genus *Medusagyne*. A more detailed molecular study of *Medusagyne*, Fay *et al.* (1997) placed that genus near to Ochnaceae and not particularly close to Caryocaraceae. Ehrendorfer *et al.* (1984) reported on the chromosome number of three species of *Caryocar* as 2n = 46. They concluded that the number and the small size of the chromosomes agreed with placement of the family in the Theales.

Systematics

Caryocaraceae Voigt, Hort. Suburb. Calcutt. 88 (1845)[1].

Caryocaraceae Szyszylowicz in Engl. & Prantl, Nat. Pflanzenfam. 3(6): 153-157 (1875).

Rhizoboleae DC, Prodr. 1: 599 (1824).

Rhizobolaceae Lindley, Nat. Syst. Bot. ed. 2: 76 (1836).

Ternstroemiaceae tribus *Rhizoboleae* Benth. & Hook., Gen. Pl. 1: 180-181 (1862).

Trees or rarely shrubs or suffruteces. Leaves trifoliolate compound, alternate or opposite; stipules 2–4, but usually early caducous or absent; lamina often coriaceous, margins often serrate, dentate or crenate, rarely entire. Inflorescences a terminal raceme or a botryoid (in *Anthodiscus*). Flowers bisexual, actinomorphic. Sepals 5(–6), imbricate, large in *Caryocar*, small and united in a cupuliform calyx with indistinct lobing in *Anthodiscus*. Petals 5(–6), imbricate, caducous, free or slightly connate at base, or united at apex to form a caducous calyptra in *Anthodiscus*. Stamens 55–750, filaments frequently caducous as a unit together with petals, usually united into a short ring at base, long and slender, usually with some shorter interior ones which are recurved, the apical portion tuberculate with minute gland-like tubercules, the sterile filaments often with spirally arranged tubercules for entire length; anthers bilocular, basifixed or attached at middle, with a broad, parenchymatous connective. Ovary superior, free 4(–6)-celled in *Caryocar*, 8–20-celled in *Anthodiscus*, each loculus with a single ovule, the ovules basal, erect, anatropous or campylotropous, bitegmic in *Caryocar*, unitegmic in *Anthodiscus*. Styles 4 or 8–20, long and slender, stigmatose at apex, simple in *Caryocar*, compound in *Anthodiscus*. Fruit a drupe, with 1–4 seeds developing in *Caryocar*, 8–20 in *Anthodiscus*, mesocarp indehiscent, usually fatty and fleshy; endocarp hard and woody, muricate, tuberculate or spinulose on outer surface, eventually splitting into 1-seeded pyrenes or mericarps, seeds often reniform, endosperm thin or lacking, the embryo with a straight arcuate or spirally twisted radicle, a fleshy hypocotyle and two small cotyledons.

A family of two genera and 26 species confined to the Neotropics from Costa Rica to southern Brazil.

[1] In Prance & Silva (1973) we were unaware of the denomination of the family in Voigt (1845) and attributed the family name to Szyzylowicz (1875).

Key to the genera of Caryocaraceae

1. Leaves opposite; styles 4, simple; ovary 4(–6)-locular, ovules bitegmic ..... 1. Caryocar
1'. Leaves alternate; styles 8–15, compound; ovary 8–15-locular, ovules unitegmic ..... 2. Anthodiscus

1. Caryocar.
Caryocar L., Mantissa plantarum 2: 247. 1771. Type: *Caryocar nuciferum* L.
Pekea Aubl., Pl. Guiane 1: 594-599. 1775. Type: *Pekea butyrosa* = *Caryocar nuciferum* L. pro parte, fruit only.
Souari Aubl., Pl. Guiane 1: 599-601. 1775. Type *Souari glabra* = *Caryocar glabrum* (Aubl.) Pers.
Barollaea Necker, Elem. Bot. 2: 322. 1790, nom. illegit.
Rhizobolus Gaertn. *ex* Schreb., Linn. Gen. Pl. ed. 8, 1: 369. 1789. Type: *Rhizobolus pekea* Gaertn. = *Caryocar nuciferum* L. pro parte, fruit only.
Acantacarix Arruda da Camara *ex* Koster, Trav. Bras. 491. 1816, nom. nud.

Large trees or rarely shrubs or suffrutices, with opposite branches. Leaves opposite, with stipules absent or present and soon caducous, usually long-petiolate but very rarely almost sessile, trifoliolate; leaflets with short petioles, pinnately nerved, the margins serrate, crenate, dentate or rarely entire, often with 2–4 stipels at base of leaflets, the stipels persistent or caducous, sometimes with 2 large and 2 small stipels. Inflorescences a terminal raceme with a short rachis, often rather corymbose; pedicels articulate at apex. Bracts seldom developed, usually none, bracteoles lateral, alternate, small, subpersistent or caducous. Flowers bisexual, large. Sepals 5(–6), imbricate. Petals 5 or rarely 6, imbricate, fused at base together with the base of the filaments and often caducous as a unit with the filaments. Stamens numerous, 55–750, exceeding the petals; filaments bent into an S in bud, those on the interior shorter and sterile or with smaller anthers, often with a row of short sterile staminodes on the interior, the basal portion of which form a glandular nectar secreting tissue; the apical portion of filaments tuberculate and entire length of smaller filaments sometimes tuberculate; anthers bilocular, oblong, introrse, dorsifixed or basifixed, longitudinally dehiscent. Ovary usually 4-locular, sometimes to 6-locular, with a single bitegmic ovule in each loculus; styles 4, long filamentous, simple. Drupe 4–6 locular, with from 1–4 loculi developing, and dehiscing into 1 seeded cocci; mesocarp thick and fatty or fleshy; endocarp woody, muricate, tuberculate or spinous on exterior; seeds reniform or subreniform, the embryo with a straight to arcuate radicle. Germination hypogeal, first leaves opposite (observed in two species). 2n = 46.

From Costa Rica and Colombia through lowland South America east of the Andes to Paraguay and the state of Paraná, Brazil, especially common in the Guianas and Amazonia; absent as a native from the West Indies.

The name is derived from the Greek *karyon, καρύδι* = nut or kernel and κορυφή = the head, crest, referring to the shape of the fruit. In Brazil most species are known as *piqui* or *pequi* or qualifications of this name. This is derived from an indigenous word meaning 'thorny covering' (Heringer 1969).

This genus is predominantly pollinated by glossophagine bats (Vogel 1968; Gribel & Hay 1993; Martins & Gribel 2007), less often birds (Melo 2001). A summary of the chemistry and medicinal uses of the family was given by Ascari *et al.* (2013). The oil in the seeds contains high amounts of the unsaturated fatty acids palmitic and oleic acids (Handro & Barradas 1971).

Key to species of *Caryocar*

1. Stipels absent or small and early caducous.
   2. Leaflet underside with conspicuously reticulate and prominent venation, usually villous, Rarely glabrous; pedicels bracteolate.
      3. Leaflets obtuse to rounded or acute at apex; small gnarled cerrado tree to 5 m, or suffrutex ..... 1.3. *Caryocar brasiliense*
      3'. Leaflets distinctly acuminate at apex; large forest trees ..... 1.16. *Caryocar villosum*
   2'. Leaflet underside with plane or prominulous venation, glabrous or with a barbate junction of midrib and veins only; pedicels usually ebracteolate except in *C. cuneatum*.
      4. Leaflets obtuse to rounded at apex ..... 1.4. *Caryocar coriaceum*
      4'. Leaflets distinctly acuminate at apex.
         5. Calyx ca. 2 cm long; corolla lobes 6–7 cm long; filaments 7–8.5 cm long; stamens over 700; Guianas and Venezuela ..... 1.14. *Caryocar nuciferum*
         5'. Calyx 4–12 mm long; corolla lobes 1–3 cm long; filaments 4–6.5 cm long; stamens not exceeding 520.

6. Pedicels bracteolate; leaf apices mucronate; northern Planalto ..... 1.6 *Caryocar cuneatum*
6'. Pedicels ebracteolate; leaf apices usually acuminate.
7. Flowers small; calyx 4–6 mm long; western Amazonia ..... 1.10. *Caryocar gracile*
7'. Flowers large; calyx 7–12 mm long.
8. Apex of pedicels and exterior of calyx tomentellous; pedicels 1–2.6 cm long, not crustaceous; leaf margins irregularly dentate, the teeth mostly spaced far apart; Peru .. ..1.2. *Caryocar amygdaliforme*
8'. Apex of pedicels and exterior of calyx glabrescent; pedicels 1.0–2.6 cm long, usually crustaceous sometimes not so; leaf margins entire or weakly crenulate.
9. Leaf margins entire or only slightly undulate.
10. Peduncles and pedicels crustaceous lenticellate; filaments usually deep red, rarely white..... 1.9. *Caryocar glabrum*
10'. Peduncles and pedicels without lenticels or sparingly lenticellate but never crustaceous; filaments always white or yellow.
11. Primary veins 8–9 pairs; peduncles round in cross section; pedicels 2.3–3.1 cm long.....1.13. *Caryocar montanum*
11'. Primary veins 10–12 pairs; peduncles square in cross section; pedicels 1.5–2 cm long.....1.11. *Caryocar harlingii*
9'. Leaf margins deeply crenulate .....1.15. *Caryocar pallidum*

1'. Stipels present and persistent.
12. Leaf underside with hirsute mass at junction of primary veins and midrib.
13. Inflorescence rachis 5–9 cm long.
14. Terminal leaflet 12–16 cm long; peduncles 12–14 cm long..... 1.9. *Caryocar glabrum*
14'. Terminal leaflet 7–11.5 cm long; peduncles 6.5–10 cm long; eastern-central Brazil.
13'. Inflorescence rachis 2.5–3.5 cm long.
15. Peduncles 4–7 cm long, conspicuously lenticellate; terminal petiolule 6–13 mm long, deeply canaliculate; leaf margins crenate; eastern-central Brazil ....1.8. *Caryocar edule*
15'. Peduncles 9–15 cm long, not conspicuously lenticellate; terminal petiolule 2–3 mm long, terete or shallowly canaliculate; leaf margins serrate; Costa Rica..... .....1.5. *Caryocar costaricense*
12'. Leaf underside entirely glabrous or with few hairs on midrib and primary veins but no hirsute mass at their junction.
16. Leaf margins deeply and conspicuously serrate.
17. Calyx lobes tomentellous on exterior; petioles usually puberulous..... .....1.7. *Caryocar dentatum*
17'. Calyx lobes glabrous, petioles glabrescent.
18. Leaves narrowly oblong; stipels small and inflated, to 3 mm long; Colombia..... .....1.1. *Caryocar amygdaliferum*
18'. Leaves elliptic; stipels large and recurved, 5–10 mm long; Amazonia and Venezuela .....1.15. *Caryocar pallidum*
16'. Leaf margins entire to slightly crenulate-serrate.
19. Leaves coriaceous; peduncle, rachis and pedicels crustaceous lenticellate; stamens ca 280; Amazonia ..... 1.9. *Caryocar glabrum*
19'. Leaves membraneous-chartaceous; peduncle rachis and pedicels sparsely lenticellate, but never crustaceous; stamens ca 60; Guianas, Amazonia, Venezuela..... ..... 1.12. *Caryocar microcarpum*

1.1. *Caryocar amygdaliferum* Mutis in Cavanilles, Ic. et Descr. Pl. 4. 37, t. 361, 362. 1798.
Type: COLOMBIA. Tolima: Mariquita, *J.C. Mutis 4450* (holotype MA-01-00661154; isotypes MA-01-00661156, US00110229; fragments at F, NY429009). Fig. 1a

Trees to 55 m tall, trunk buttressed up to 3 m, the young branches sparsely puberulous-glabrescent. Leaves trifoliolate; petioles 2.5–11 cm long, glabrescent, terete; leaflets shortly petiolulate, the terminal petiolule 5–7 mm long, the lateral petiolules slightly shorter than the terminal one, all petiolules sparsely puberulous, shallowly canaliculate; stipels to 5 mm long, ellipsoid, inflated, persistent; laminas elliptic to oblong, slightly asymmetrical, acuminate at apex, the acumen 1–1.5 cm long, cuneate to subcuneate and often markedly unequal at base, unevenly coarsely serrate at margins, glabrous on both surfaces, terminal lamina 7.5–12 × 2.5–5.5 cm, lateral laminas slightly smaller than the terminal one; primary veins 10–11 pairs, plane to prominulous beneath; venation prominulous beneath. Peduncles ca 3.5–7 cm long, glabrous. Inflorescences clustered racemes; rachis tomentose, the pedicels elongate, ebracteolate. Calyx cupuliform, ca 6 mm long, glabrous on exterior; lobes 5, small, rounded the margins ciliate. Corolla lobes 5, ca 2–2.5 cm long, oblong, glabrous, greenish-yellow. Stamens numerous, ca 200, the filaments shortly united at base in a ring, but into groups, white, sparsely pubescent, apical portion tuberculate, innermost filaments much shorter than the rest; anthers small. Ovary globose, glabrous on exterior, 4-locular. Styles 4, filamentous, shorter than filaments. Fruit globose-ellipsoid, ca 5.5 cm long, exocarp glabrous, smooth; pericarp thick, fleshy; mesocarp and endocarp enveloping the seed to form an ovoid stone; the exterior of mesocarp not seen, the interior enveloping the endocarp tubercules; endocarp with numerous flattened tubercules ca 5 mm long, and a hard, woody interior ca 1 mm thick, glabrous within.

Additional material examined: PANAMA. DARIÉN: Punta Guayabo Chiquita, 23.VI.1957, *Stern & Chambers 161* (MO). COLOMBIA. ANTIOQUIA: 36 km N. of Barancabermeja, 100 m, 4.III.1967, *de Bruijn 1578* (COL, MO, NY, U, US, VEN); mun. de Caucasia, road to Nechí, 24 km from Caucasia-Planeta Rica road, 08°04'N, 75°05'W, 60 m, 21.III.1987, *Zarucchi et al. 4911* (COL, INPA, MO, NY). BOLÍVAR: Valle de Magdalena, Cimitarra, km 3, 24.VII.1954, *Lamb 132* (COL, US). La Raya, Culebra Caño Caribon between Ríos Canca and Magdalena, 80 m, 5.V.1987, *Gentry 57382* (K, MO). CAQUETÁ: Florencia, XII.1930, fr., *Pérez-Arbeláez 638* (COL, US). CHOCÓ: Riosucio, 07°29'13"N, 76°50'53"W. 50-200 m, 14.XI.1997, *Cárdenas 818* (COAH, MO). SANTANDER: Trocha del Oponcito al Opón, 29.VIII.1953, fl. and fr., *C. Romero 4341* (COL).

The pulp of the fruit is edible and has also been used as a fish poison.

This species has been confused with *C. amygdaliforme* Don, for details and differences see under that species. *Caryocar amygdaliferum* is easily distinguished from related species by the larger persistent, inflated stipels.

The species is present in forests of the Magdalena river valley of Colombia and Panama.

Illustrations in Mutis (1798) as above; Wittmack, Martius, *Flora brasiliensis* 12(1) t. 69, X-XI.1886, fruit.

Local names: *achotillo, mani, cagui, chalmagra*.

Caryocar amygdaliferum is listed as vulnerable: VU a2acd in Colombia, Calderon (1998).

1.2. *Caryocar amygdaliforme* G. Don, Gen. Syst. 1: 654. 1831.
Caryocar amygdaliferum sensu Ruiz & Pavon, Fl. Peru 5, *t. 479*, non *C. amygdaliferum* Mutis.
Type: PERU. HUÁNUCO: Chicoplaya, 1778, *Ruiz & Pavon* (holotype MA, frag F V0053241; isotypes BM000603043, G00226240). Fig. 1b

Trees to 25 m tall, the young branches puberulous, becoming glabrous with age. Leaves trifoliolate; petioles 3–7 cm long, sparsely puberulous soon glabrescent, slightly flattened, the leaflets shortly petiolulate, terminal petiolule 5–7 mm long, lateral petiolules more or less equal to the terminal one, all petiolules sparsely puberulous, shallowly canaliculate; stipels absent; laminas elliptic, symetrical or only slightly asymetrical, acuminate at apex, acumen 5–12 mm long, rounded and unequal at base, irregularly dentate at margins, teeth often widely separated, large and few, 1–17 per side, glabrous above, glabrous except for few hairs on midrib and at junction with primary veins, the terminal lamina 11–16 × 6–8 cm, lateral laminas slightly smaller than the terminal one; primary veins 10–12 pairs, prominulous above, prominent beneath; venation prominulous beneath. Peduncles 7–9.5 cm long, sparsely puberulous when young, terete. Inflorescences clustered racemes, 12–20-flowered, the rachis 2–2.6 cm long, puberulous-tomentellous; flowering pedicels 3–5 cm long, puberulous, especially towards

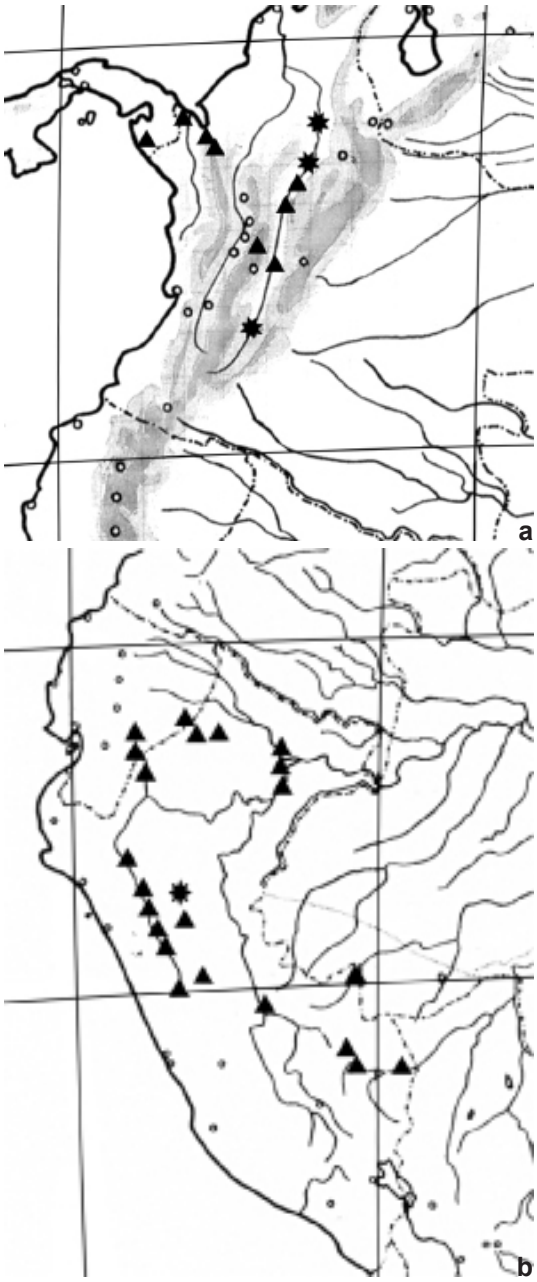

Figure 1 – a-b. Distribution of *Caryocar* species – a. *C. amygdaliferum*, stars = known distribution in 1973; b. *Caryocar amygdaliforme*, star = known distribution in 1973. (based in Prance & Silva (1973)).

the apex beneath the flower, ebracteolate. Calyx cupuliform, 5–7 mm long, sparsely puberulous on exterior, tomentellous towards base; lobes 5, rounded, with ciliate margins. Corolla ca 2.5 mm long; lobes oblong. Stamens numerous, filaments shortly united at base into a caducous unit, but not into groups, the outer ones 4–6.5 cm long, the apical portion tuberculate, the inner filaments much shorter, 1.5–2.5 cm long, tuberculate for entire length; anthers small. Ovary globose, 4-locular, glabrescent on exterior. Styles 3–4, filamentous. Fruit not seen.

Additional material examined: ECUADOR. MORONA-SANTIAGO: Centro Shuar Yukutais, 02°30'S, 78°08'W, 900 m, 12.III.1990, fl., *Bennett 4136* (K, MO, NY). PERU. AMAZONAS: Valle del Río Santiago, 65 km N of Pinglo, Quebrada Caterpiza, 200 m, 7.II.1980, *Huashikat 1995* (MO, NY). Huánuco: Pachitea, Codo de Pozuzo, Río Pozuzo, 450 m, 18.X.1982, *Foster 9276* (MO, NY). JUNIN: Prov. Satipo, Reserva Forestal Satipo, 750 m, 7.XII.1962, fl., *Vasquez 5* (F, NY, US). LORETO: Requena, Río Ucayali, Jenaro Herrera, 7.XII.1977, *Gentry et al. 21177* (F, MO, NY). MADRE DE DIOS: Río Manú, Parque Nacional del Manú, Pakitza Station, 350 m, 19.XI.1980, *Foster 5767* (F, NY). PASCO: Oxapampa, 787 m, 12°03'54"S, 75°32'56"W, 19.V.2004, *Perea 1219* (MO, USM). SAN MARTÍN: Juan Juí, alto Río Huallaga, 400 m, X.1934, *Klug 3907* (BM, F, GH, K, MO, NY, S, US). UCAYALI: Bosque Nacional Von Humboldt, km 8, Pucallpa-Tingo Maria, 08°40'S, 75°00'W, 270 m, 9.II.1981, *Gentry et al. 31137* (MO).

The nomenclature of this species is complicated and confusing and so it is worth repeating here. The name *C. amygdaliforme* was first published by George Don where he refers to its origin from Ruiz and Pavon's unpublished Flora of Peru 5 t. 570. Wittmack (1886) checked the manuscripts of Ruiz and Pavon at Madrid, and even published their description. He pointed out that Ruiz and Pavon in fact labelled their material as *C. amygdaliferum* (Cav.) Mutis not *C. amygdaliforme*. That is, Ruiz and Pavon considered their material as part of Mutis' species *C. amygdaliferum* rather than a new species. Wittmack pointed out the considerable differences between the description of Mutis and the unpublished one of Ruiz and Pavon, but he still accepted Ruiz and Pavon's opinion that their Peruvian material was part of the Colombian species *C. amygdaliferum*, and he attributed the differences to gross misinterpretation by Ruiz and Pavon. Don on the other hand clearly regarded the Ruiz and Pavon material as distinct since he gave a synopsis of the 6 species of *Caryocar* known to him. Species No 5 was *C. amygdaliferum* Mutis, and species No 6 was "*C. amygdaliforme* (Ruiz et Pav. Fl. Per. 5. t. 570)." In fact the Ruiz and Pavon plate is labelled 470 not 570. Don's name, *C. amygdaliforme* is followed by a synoptic description quite long enough to recognize the

species and to be considered valid. Since Don clearly regarded *C. amygdaliforme* as different from *C. amygdaliferum*, since the Ruiz and Pavon manuscript is unpublished, and since Don provided an adequate description of this species, he must be regarded as the author of *C. amygdaliforme*. While it is unfortunate to have two epithets in the same genus as similar as *amygdaliferum* and *amygdaliforme*, it is necessary to accept them both as valid.

Although Wittmack treated *C. amygdaliferum* of Mutis and the Ruiz and Pavon description as the same species, he gave a list of quite significant differences between the two descriptions, which he attributed to inaccurate observations by the authors. While some of the differences are due to misinterpretation by the authors, others, such as the presence of stipels in *C. amygdaliferum* and the absence of them in *C. amygdaliforme*, are quite genuine. I have studied both the Mutis and Ruiz and Pavon herbarium material as well as more recent collections matching both types. From this material it is obvious that these are separate species and they are also allopatric. A table of differences between these two species was given in Prance & Silva (1973).

The species is widespread in Amazonian Peru and Ecuador.

Local name: Peru: *almendra.*

Caryocar amygdaliforme is listed as Endangered (E) in Walter & Gillett (1998, B1+2c).

1.3. *Caryocar brasiliense* Cambessèdes in Saint-Hilaire, Fl. Bras. Mer. 1: 322, t. 67 bis. 1828.
Type: BRAZIL. MINAS GERAIS: São Bento, *A. Saint-Hilaire 625* (lectotype MPU014414; isolectotypes F0053242, P01900574). Fig 2a

Trees to 10 m tall, usually smaller and with a gnarled trunk up to 30 cm diameter, sometimes a low shrub or suffrutex, the young branches tomentellous soon glabrescent with age. Leaves trifoliolate; petioles 1–10.5 cm long or rarely the apical leaflets subsessile, tomentose, terete; leaflets shortly petiolulate, the terminal petiolule 4–8 mm long, the lateral petiolules 1–4 mm long, all petiolules tomentose, terete or shallowly canaliculate; stipels absent; laminas ovate elliptic, often markedly asymetrical, rounded serrate at apex, rounded and markedly unequal at base, coarsely crenate at margins, sparsely villous above or rarely almost glabrous, usually villous beneath, rarely sparsely hirsute, terminal lamina 10–18 × 8–12 cm, lateral laminas equal or smaller than the terminal one; primary veins 10–13 pairs, slightly impressed or plane above, prominent beneath; venation extremely prominent beneath. Peduncles 4–10 cm long, usually densely tomentose, rarely only puberulous, flattened, canaliculate. Inflorescences clustered racemes, the rachis 2.5–5.5 cm long, usually tomentose, rarely only puberulous; flowering pedicels 1–5 cm long, tomentose to puberulous, with 2 membraneous bracteoles on upper portion. Calyx broadly cupuliform, 10–13 long, sparsely puberulous on exterior, the base often tomentose, the lobes 5(–6), rounded. Corolla 1.8–3 cm long, the lobes 5–6, oblong, yellow or yellow within and orangish red on exterior. Stamens numerous, ca 270–330; filaments shortly united at base into a caducous ring, 3.5–5 cm long, yellow, apical portion tuberculate, innermost filaments shorter, 1.5–2 cm long, small. Ovary globose, usually 4-locular, rarely to 6-locular, glabrous on exterior. Styles 4–6, usually 4, ca 5 cm long, glabrous, filamentous. Fruit ovoid-globose, ca 4–5 cm long, 4–5 cm broad, usually 2-locular; exocarp glabrous, smooth, without lenticels or sparsely lenticellate; pericarp thick, fleshy, remaining attached to mesocarp; mesocarp and endocarp enveloping seed to form an ovoid stone ca 2.5 cm broad, exterior of mesocarp smooth, the interior enveloping endocarp spines; endocarp with numerous fine spines 2–3 mm long and hard, thin, woody, the inner portion ca 1 mm thick, glabrous within. 2n = 46.

Key to subspecies of *Caryocar brasiliense*

1. Peduncles and pedicels densely tomentose to tomentellous; upper surface of leaves densely hirsutulous, rugose; lower surface tomentellous; small to medium sized trees.....1.3.1. *Caryocar brasiliense* subsp. *brasiliense*
1'. Peduncles and pedicels glabrous or sparsely puberulous; upper surface of leaves glabrous or sparsely hirsutulous and plane not rugose, lower surface sparsely hirsutulous; low suffrutices 30–80 cm tall, or shrubs .....1.3.2. *Caryocar brasiliense* subsp. *intermedium*

1.3.1. *Caryocar brasiliense* subsp. ***brasiliense***.

Fig. 2a

Additional material examined: BOLIVIA. BENI: 37 km E of Riberalta, road to Guayaramerín, 11°05'S, 65°45'W, 230 m, 21.V.1982, *Solomon 7737* (MO, NY). SANTA CRUZ: Chiquitos Prov., 10 km E of Robore, 18°24'S, 60°37'W, 200 m, 12.XI.1996, fl., *Jardim & Mamani 3668* (K, MO). BRAZIL. PARÁ: Gorotire at Rio Fresco, 07°47'S, 51°07'W, 200 m, 17.I.1983, *Gottsberger & Posey 139-17183* (NY); near Redenção, Fazenda Chocolate, 08º21'S, 50º00'W, 18.VII.1993, fl., *Ratter et al. 68678* (E, K). RONDÔNIA: 4 km from Vilhena, 12°45'S, 60°10'W, 25.X.1979, *Vieira et al. 634* (INPA, NY, US). TOCANTINS: 56 km N. of Gurupí, on Belém-Brasília highway, 11°28'S, 48°53'W, 13.XI.1997, *Ratter et al. 7974* (E, K). DISTRITO FEDERAL: 15 km SW of Brasília, road to Goiania, IX.1965, *Irwin et al. 8633* (INPA, NY). GOIÁS: Mun. Niquelândia, Fazenda Traira, 8.VIII.1995, *Marquete et al. 2209* (K). MATO GROSSO: Diamantina, road Cuiabá to Sinop, 160 km S of Sinop, 13°12'S, 56°00'W, 17.IX.1985, *Cid Ferreira 6058* (INPA, K, NY); Chapada das Guimarães, above Cachoeira Furada, Reserva Buriti, 12.X.1973, fl., *Prance et al. 18826* (INPA, MO, NY, UFMT, US). MATO GROSSO DO SUL: Corumbá, Serra do Amolar, Morro da Penha, 19.009199, -57.65330, 200 m, 20.X.2002, *Bortolotto et al. 1209* (COR). BAHIA: Cocos, road Cocos to Caribe, 14 km from Cocos, 14°24'S, 44°29'47"W, 18.IV.2001, *Jardim 3628* (CEPEC, NY). MINAS GERAIS: Itumirim, 9 km W of Itutinga, Highway 265, 930 m, 27.II.1976, *Davidse & Ramamoorthy 10758* (MO, US). SÃO PAULO: Moji-Guaçu, 15 km N of Padua Sales, XII.1959, *Eiten & Campos 1504* (NY, US). PARANÁ: Jaguariahyva, 10.IV.1910, *Dusén 9633* (MO, S); Piraí do Sul, -24.52610, -49.94860, 17.IV.1987, *Kuniyoshi et al. 5159* (EFEC); Fazenda Charlote, Rio Iapó Tibagi, 750 m, 11.XII.1989, fl., *Pimenta FUEL7822* (FUEL, K).

The many uses of this species were summarised in Araújo (1995). The fruit yields an edible pulp and a vegetable oil. The oil is also used in the cosmetic industry. A complete analysis of the oil content of the mesocarp and seeds of this species is given in Handro & Barradas (1971). This is an important tree for the central Brazilian Indians and often grown by them for the edible fruit and for the yellow dye used to paint themselves. It has been semidomesticated by various tribes for example the Kuikuro of the Rio Xingu area who grow *C. brasiliense* in family orchards (Smith & Fausto, 2016). The fruit is also much used in traditional medicine.

The pollination of this species is mainly by glossophagine bats (Gribel & Hay 1993). Diurnal birds may play a role as secondary pollinators in *Caryocar brasiliense* (Melo 2001). Ants collect nectar from extra-floral nectaries located on buds at the apex of the plants of *C. brasiliense*, increasing herbivore deterrence and reproductive output (Oliveira 1997). A draft genome sequence of this species was published by Nunes *et al.* (2019) being the first for the Caryocaraceae.

The species is present in Brazil south to Paraná and Paraguay, cerrados of the Planalto.

Illustrations in Wittmack, Martius, *Flora brasiliensis* 12(1) t. 73. 1886; Perdiz *et al.* 2012: 111.

Local names: *Amêndoa de espinho, grão-de-cavalo, pequi, pequiá, pequizeiro, piqui*.

Caryocar brasiliense subsp. *brasiliense* is least concern (LC). Araújo (1995) questioned whether the over exploitation of the fruits of this species will pose a threat to its conservation, but this is unlikely.

1.3.2. *Caryocar brasiliense* subsp. ***intermedium*** (Wittmack) Prance & Silva, Fl. Neotrop. Monogr. 12: 26. 1973.

Caryocar intermedium Wittmack, Mart. *Fl. bras.* 12(1): 352. 1886.

Caryocar brasiliense Cambessèdes var. *planifolium* forma *dentata* Chodat & Hassler, Bull. Herb. Bois. II. 3: 809 (1903). Type: PARAGUAY. Sierra de Maracaya, 1898-99, *Hassler 5311* (holotype G00106702).

Type: BRAZIL. S. Ignacio (? Minas Gerais), *Sellow 2191* [lectotype of Prance & Silva (1973) BM000603032; isolectotype F0BN009698].

Fig. 2a

This subspecies differs from subspecies *brasiliense* in the glabrous or sparsely puberulous pedicels and peduncles, in the glabrous or only sparsely hirsute and plane upper surface of the laminas, in the sparsely hirsute undersurfaces of the laminas, and in the lower growth form often being a low suffrutex.

Additional material examined: BOLIVIA. BENI: Iténez, Serrania de San Simón, 200 m, 14°25'S, 62°03'W, 19.VII.1993, fl., *Quevado et al. 954* (K, MO, NY, USZ). SANTA CRUZ: Velasco, PN Noel Kempff, Las Gamas, 14°48'41"S, 60°23'45"W, 900 m, 30.III.1993, *Killeen et al. 4917* (K, MO, USZ). BRAZIL. RONDÔNIA: Vilhena, -12.75, -60.16666, 25.X.1979, *Vieira 640* (INPA, MO, NY). MATO GROSSO DO SUL: BR-163, Sidrolândia, 27.X.1962, fl., *Hatchsbach 25271* (MBM, NY, US); Tacurú, 5 km W of Tacurú road to Iguatemí 23°45'S, 55.45'W, 16.XII.1983, *Callejas et al. 1961* (K, NY). MINAS GERAIS: Triángulo Region, *Goodland 701* (MO, NY). SÃO PAULO: N of Moji-Guaçu, 3.5 km NNW of Padua Sales, 600 m, 21.IX.1960, fl., *Eiten et al. 2369* (F, NY, UC). PARANÁ: *Dusén 15968* (L, MO, NY, P, S, UC). Jaguariaiva, Rio das Mortes, 25.XI.1980,

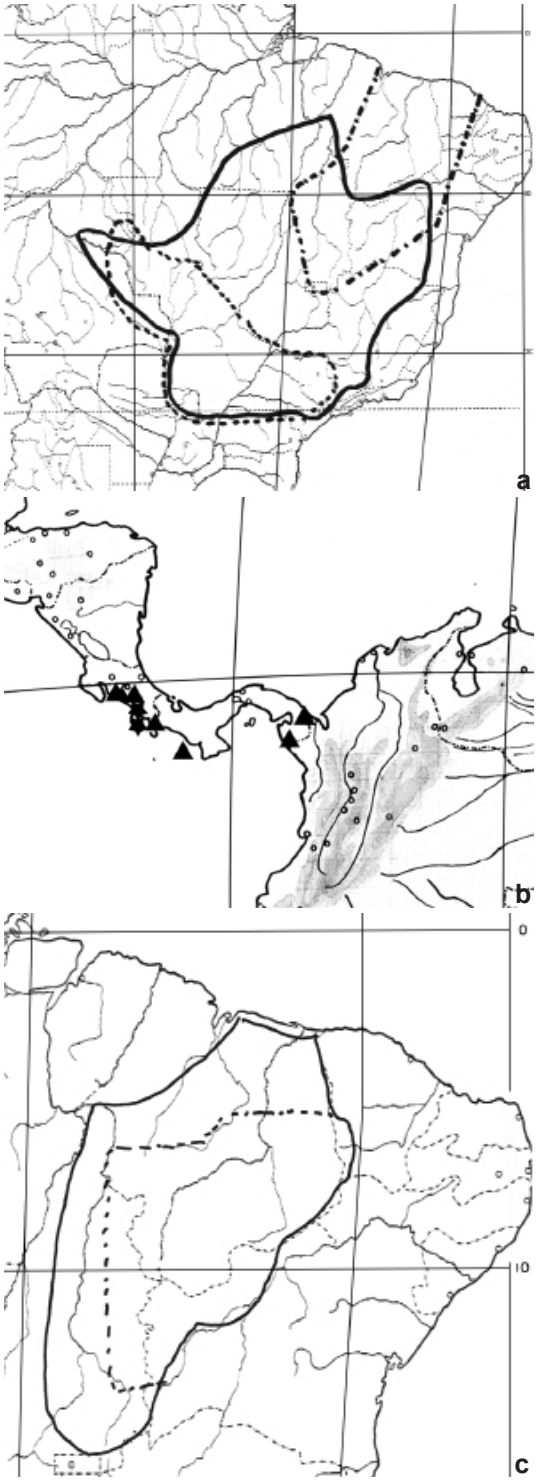

Figure 2 – a-c. Distribution of *Caryocar* species – a. solid line = *C. brasiliense* subsp. *brasiliense*, dotted line = *C. brasiliiense* subsp. *intermedium*, dot/dash line = *C. coriaceum*; b. *C. costaricense*, stars = known distribution in 1973; c. *C. cuneatum*, dotted line = 1,973 known distribution. (based in Prance & Silva (1973))

Hatschbach 43386 (MBM, MO, US). PARAGUAY: no date, *Hassler 4920* (A, BM, G, K, MO, P, S, UC); Ambay, PN Cerro Corá, 4.X.1980, *Fernández-Casas et al. 4061* (NY).

Towards the southern part of the range of *C. brasiliense* there is a definite tendency to a more glabrous peduncle, pedicel and leaves, the leaves are thinner and less rugose above, the plants are often suffruticose rather than trees, the leaflets tend to be narrower, and the petioles shorter. None of the above characters is diagnostic and there is considerable overlap in any one character, but since there are several correlated differential characters involved, and since there is a distinct geographical correlation *C. brasiliense* is subdivided into the 2 subspecies.

The species is found in Southwestern Brazil and adjacent Bolivia and Paraguay.

Caryocar brasiliense subsp. *intermedium* is Least concern (LC), however *Caryocar brasiliense* is the only tree species protected by federal regulations in Brazil and it is used for nest sites by the rare stingless bee species *Melipona quadrifaciata* (Antonini & Martins (2003).

1.4. *Caryocar coriaceum* Wittmack, Mart. *Fl. bras.* 12(1): 352. 1886.

Type: BRAZIL. CEARÁ: Vila do Crato, *Gardner 1494* (lectotype of Prance & Silva 1973, K000741715; isolectotypes BM000603035, CGE, G00226562, G00226564, G00226563, GH00062679, GH00062680, V0053243F, K000432509, K000432510, L0012438, NY00429010, NY00429011, OXF, P01900572, S10-7827, US00110230, W0047713, frag F V0053243). Syntypes: BRAZIL. BAHIA: Rio São Francisco, 1838, *Blanchet 2876* (V0053244F, G0022693, G00226594, K000432506, P, W1889012159); CEARÁ: without locality, 1838, *Gardner 1495* (G00226562, K, US01049834).

Fig. 2a

Tree to 15 m tall, to 35 cm diam., the young branches glabrous, conspicuously lenticellate. Leaves trifoliolate; petioles 1.5–4 cm long, glabrous or sparsely puberulous soon glabrescent, terete; leaflets shortly petiolulate, the terminal petiolule 1–3 mm long, lateral petiolules shorter than the center one, petiolules shallowly canaliculate, glabrous or sparsely puberulous soon glabrescent; stipels absent: laminas ovate, often slightly asymetrical, rounded or retuse at apex, subcuneate and usually markedly unequal at base, serrate to crenate at margins, glabrous on both surfaces,

terminal lamina 5–10 × 3.5–7 cm, lateral laminas equal to or smaller than the terminal one; primary veins 8–10 pairs, prominulous above, prominent beneath; venation prominulous beneath. Peduncles 2.5–8.5 cm long, glabrous, terete. Inflorescences clustered racemes, 10–16-flowered, rachis 1.5–4 cm long, glabrous; flowering pedicels 2–2.5 cm long, the lower ones longer than the upper ones, glabrous; bracteoles caducous. Calyx broadly cupuliform, 8–9 mm long, glabrous on exterior, the lobes 5, rounded. Corolla 2–2.3 cm long; lobes 5, oblong, white, sometimes tinged light red on upper half of exterior. Stamens numerous, ca 300; filaments shortly united at base into a ring, but not in groups, 3.2–4 cm long, white, the apical part tuberculate, the inner ones only slightly shorter than the outside ones, the anthers small, yellow. Ovary globose, 3–4-locular, glabrous on exterior. Styles 3(–4), exceeding filaments in length, glabrous, filamentous. Fruit ovoid; mesocarp and endocarp enveloping the seed to form an ellipsoid stone ca 3.8 cm long, the mesocarp enveloping the endocarp spines; endocarp with numerous very fine needle-like spines ca 5 mm long, and a thin hard woody interior ca 1 mm thick, glabrous within.

Additional material examined: BRAZIL. TOCANTINS: 4 km from Monte de Carro, road to Ponte Alta do Tocantins, 2.XI.1997, *Bridgewater 777A* (E, UB). BRAZIL. GOIÁS: Terezina, estrada Alta Paraiso, 10.X.1979, fl., *Heringer 2454* (K, MO, NY, UB). BRAZIL. BAHIA: Rio São Francisco, 1838, *Blanchet 2876* (V0053244F, G0022693, G00226594, K000432506, P, W1889012159); 2 km from Riachão das Neves, road to Barreiras, 24.VII.1998, *Ratter 8034* (E, UB). CEARÁ: without locality, 1838, *Gardner 1495* (G00226562, K, US01049834); Serra Araripe, Taboca, 25.III.1936, fr., *Luetzelburg 26521* (EAC, F, M, P); Ch. Araripe, Cariri, Crato, -7.364722, -49.13333, 19.IX.2008, fl., *Saraiva* (EAC). MARANHÃO: PN Chapada das Mesas, Carolina, -6.94916, -47.38055, 18.X.2015, fr., *Sevilha 5314* (CEN). PERNAMBUCO: Sitio Mata Grande, Moreilândia, 11.XII.2017, fl., *F.M. Silva HCDAL13309* (HCDAL). PIAUÍ: Fazenda Açude, Capitão de Campos, -4.45666, -41.94250, 17.II.2006, fl., *Oliveira 2116* (UFP). Uruçuí, 7.VII.2017, fl., *Câmara IFN265391* (UB).

The edible fruit also yields a comestible oil. The importance of this species as a source of income in northeast Brazil from the fruit and the oil is emphasised and analysed in Sousa Júnior *et al.* (2013). The oil extracted from the fruits is much used in popular medicine as an anti-inflammatory agent to treat colds and lung infections (Serra *et al.* 2020).

The species is distributed in Northern and eastern part of the Planalto of central Brazil.

Illustrations in Perdiz *et al.* (2012: 112).

Local name: *Pequi branco, piqui.*

Caryocar coriaceum is listed as rare (R) in Walter & Gillett (1997). Now Endangered on IUCN list (EN) A1a+2c.

1.5. ***Caryocar costaricense*** Donnell Smith, Bot. Gaz. 55: 431. 1913.

Type: COSTA RICA. PUNTARENAS: Rio del Volcán, Valle Disquís, *Pittier 12115* (holotype US00110232; isotypes NY00429008, US00110231, frag. F V0053239). Fig. 2b

Tree to 50 m tall, the trunk buttressed to 1.5 m, the young branches sparsely puberulous-glabrescent. Leaves trifoliolate; petioles 4.5–12 cm long, sparsely puberulous-glabrescent, terete; leaves shortly petiolulate, the terminal petiolule 2–3 mm long, the lateral petiolules equal to the terminal one; the petiolules sparsely puberulous-glabrescent, terete; stipels persistent, to 1 cm long, inflated; laminas oblong, slightly asymetrical, acuminate at apex, acumen 10–15 mm long, rounded to subcuneate and unequal at base, serrate at margin, glabrous above, glabrous beneath except for hirsute mass in axils of primary veins, terminal lamina 13–16.5 × 6–7.5 cm, lateral laminas slightly smaller than the terminal one; primary veins 10–12 pairs, plane or shallowly impressed above, prominent beneath; venation plane to prominulous beneath. Peduncles 9–15 cm long, sparsely puberulous-glabrescent, terete. Inflorescences clustered racemes, ca 30–35-flowered, rachis 2.5–3.5 mm long, sparsely puberulous; flowering pedicels 2–3.5 cm long, sparsely puberulous.

Bracteoles 2, caducous. Calyx cupuliform, 6–7 cm long, sparsely puberulous on exterior; lobes 5, with ciliate margins, rounded. Corolla 2–2.8 cm long; lobes 5, oblong, glabrous, yellow. Stamens numerous, ca 150; filaments shortly united at base but not into groups, 4–5 cm long, yellow, tuberculate towards apex; anthers small. Ovary globose, 4-locular, glabrous on exterior. Styles 3–4, filamentous, glabrous, ca 2 cm long. Fruit not seen.

Additional material examined: COSTA RICA. PUNTARENAS: above Palmar Norte, 5.II.1951, fl., *Allen 5840* (BM, EA, F, MEXU, UC, US, WIS). Osa, 09°09'36"N, 83°43'12"W, 100-200 m, 14.IV.1988, *Zamora et al. 1494* (CR, MO). SAN JOSÉ: Res. Biol. Carara, Lalo Barbosa, 09°45'40"N, 84°31'50"W, 300 m, 16.III.1990, fl., *Zúñiga & Jiménez 131* (K, MO). PANAMA. CHIRIQUÍ: 08°21"N, 82°59'W, 24.II.1973, *Croat 22176* (MO). DARIÉN: Punta Guayabo, Chiquita,

23.VI.1957, *Stern 5192* (US). VERAGUAS: Montijo, 07°32'40"N, 81°48'08"W, 120 m, 12.II.2005, *Ibáñez & León 4253* (MO). SAN BLAS: above Puerto Obaldia, 18.VIII.1971, *Gentry 1482* (MO).

This species is important for its commercially used timber. The anatomical and mechanical properties of the wood was studied in detail by Barghoorn & Renteria (1967). The wood is used for general and marine construction, heavy flooring, railway sleepers, boat parts, furniture components; it is especially suitable where hardness and high wear resistance are needed.

This species is the most northern reaching species of *Caryocar* being the only one in Central America. It is noted that the flowers have a strong garlic smell as is reflected in some of the local names.

The species is known only from Costa Rica and adjacent Panama. High forest.

Local names: *ajo, ají, ajillo, almendro de bajo, almendron, caballo-kup*.

Caryocar costaricense is listed on CITES Appendix II to control use of the commercial timber. Endangered (EN) A2cd: Barstow (2018). EN.

1.6. *Caryocar cuneatum* Wittmack, Mart. *Fl. bras.* 12(1): 352. 1886. Fig. 2c

Caryocar brasiliense var. *planifolium* Wittmack, Mart. *Fl. bras.* 12(1): 353. 1886. Type: BRAZIL. GOIÁS: between Cavalcante & Conceição, *Burchell 7929-2*; (isotype K000432512).

Type: BRAZIL. GOIÁS: Porto Imperial, *Burchell 8749-5* (holotype, B lost; lectotype, here designated, K000432511).

Tree to 15 m tall, to 35 cm diameter, the young branches glabrous. Leaves trifoliolate; petioles 3.5–7 cm long, glabrous, longitudinally striate; leaflets shortly petiolulate, the terminal petiolule 3–7 mm long, the lateral petiolules shorter than the terminal one, the petiolules with a few sparse hairs, soon glabrescent, terete to shallowly canaliculate; stipels absent; laminas oblong-ovate, slightly to markedly asymetrical, apiculate at apex, the acumen 2–5 mm long, cuneate to subcuneate at base, serrate crenulate at margins, glabrous above, glabrous beneath except for sparse hairs on midrib and hirsute mass at junction of midrib with primary veins, terminal lamina 8–12 × 4.5–9 cm, lateral laminas slightly smaller than the terminal one; primary veins 9–11 pairs, prominulous above, prominent beneath; venation prominulous beneath. Peduncles 4–9.5 cm long, glabrous, sparsely lenticellate, terete. Inflorescences slightly elongated racemes, the rachis 2–7 cm long, glabrous; flowering pedicels 1.5–5.5 cm long, with deltoid, membraneous, caducous bracteoles on upper portion. Calyx broadly cupuliform, 9–11 mm long, glabrous on exterior; lobes 5, rounded, the margins ciliate. Corolla 2.5–3 cm long; lobes 5, oblong, glabrous, white sometimes tinged reddish on exterior towards apex. Stamens numerous, ca 250–400, the filaments shortly united into a caducous ring at base, but not into groups, outer one 4–6 cm long, white, apical portion tuberculate, inner row much shorter, ca 2 cm long, tuberculate for entire length; anthers small. Ovary globose, glabrous, usually 4-locular. Styles 3–4, glabrous, filamentous, exceeding filaments in length. Fruit ellipsoid, ca 5 cm long; exocarp smooth, glabrous, not enveloping seed to form a stone; exterior of mesocarp smooth, the interior enveloping endocarp spines; endocarp with numerous fine needle-like spines ca 6 mm long and a hard, thin woody interior ca 1.5 mm thick, glabrous within.

Additional material examined: BRAZIL. PARÁ: Alto dos Montes, Araguaia, 17.VI.1953, fl., *Fróes 29877* (IAN). TOCANTINS: Posto Indígeno São José, 20 km W of Tocantinópolis, 8.IX.1983, fl., *Balick 1582* (CEN, NY, SPF); Serra de Mamoneira, W of Filadélfia, 2.VIII.1964, fl., *Prance & Silva 58515* (INPA, K, NY, P, U, UB, US); km 8 Palmeirópolis-Balsa do Coronel, 380 m, -13.049166, -48.314722, 12.VII.2007, fl., *Pereira-Silva 11950* (CEN); posto indígeno São José, 20 km W of Tocantinópolis, 8.IX.1983, fl., *Balick 1582* (CEN, NY, SPF). BRAZIL. BAHIA: Cristópolis, -12.24, -44.28, 15.VII.2017, *Moura IFN-68913111.2* (UB). MARANHÃO: Ilha de Balsas, between Rios Balsas and Parnaiba, 35 km S of Loreto, 07°23'S, 45°03'W, 22.IX.1963, fl., *Eiten 5391* (G, US); 60 km W of Caxias, BR-135, km 490, 20.X.1980, fl., *Daly et al. 724* (INPA, K, NY, US). PIAUÍ: mun. Sete Cidades, PN Boqueirão, 13.IX.1977, fl., *Barroso 109* (RB); Guadalupe, Fazenda Gado Bravo, -6.80515, -43.56355, 9.X.1973, *Ramalho 282* (HST, HUCPE, PEUFR). GOIÁS: Boa Esperança, VIII.1912, fl., *Luetzelburg 1446* (M); 6 km NE of Posse, 23.XI.1996, fl., *Pereira & Alvarenga 3270* (K, UFG).

The fruit is edible and yielding an edible oil.

This species is close to *C. coriaceum* and has been much confused with it, but it differs in the apiculate leaf apices, the tuft of hair at the junction of the midrib and primary veins on the lower surface of the leaf, the larger leaves and in the more elongate inflorescence.

The species is present in Northern part of Planalto of central Brazil. Woodlands.

Local name: *Pequizeiro*.

1.7. *Caryocar dentatum* Gleason, Bull. Torrey Club 60: 380. 1933.
Type: BRAZIL. RONDÔNIA: Calama, Nov-Dec 1931, fr., *Krukoff 1294* (holotype NY00429012; isotypes A00062681, BM000603044, F0053245F, G00226262, K000423513, MICH1192001, MO1913789, NY00429013, P01900570, S-R-11446, U0000974, UC497826). Fig. 3a

Tree to 20 m tall, young branches puberulous soon glabrescent. Leaves trifoliolate; petioles 2–7 cm long, tomentellous when young, soon puberulous, then glabrescent, terete; leaflets shortly petiolulate, terminal petiolule 3–9 mm long, lateral petiolules slightly shorter than the terminal one, petiolules tomentellous when young, soon puberulous, shallowly canaliculated; stipels small, 1–2 mm long, subpersistent, recurved; laminas oblong or oblong-elliptic, sometimes slightly asymetrical, acuminate at apex, acumen 7–13 mm long, subcuneate at base, deeply serrate at margins, glabrous above except for puberulous midrib, glabrous beneath except for puberulous primary veins and sparsely puberulous and hirsute midrib especially in axils of primary veins, terminal lamina 7.5–11 × 3–5.2 cm, lateral laminas slightly smaller than the terminal one; primary veins 10–13 pairs, plane or prominulous above, prominent beneath; venation conspicuous but more or less plane and minutely puberulous beneath. Peduncles 3–6 cm long, terete, tomentellous to puberulous glabrescent. Inflorescences clustered racemes, 12–20 flowered, rachis 2–3.5 cm long, tomentellous or puberulous; flowering pedicels 1–1.5 cm long, puberulous, ebracteolate. Calyx cupuliform, ca 5 mm long, tomentellous-puberulous on exterior; lobes 5, rounded, with ciliate margins. Corolla lobes oblong, 2–2.8 cm long. Stamens numerous, ca 100, the filaments shortly united at base into a single caducous unit, but not into groups, the outer ones ca 6 cm long, the apical portion tuberculate, the innermost filaments much shorter ca 1.5 cm long, tuberculate for entire length. Ovary globose, 4 locular, glabrous on exterior. Styles 4, ca 6 cm long, filamentous, glabrous. Fruit with ellipsoid stone; endocarp spinous, the spines thin, 1.5–1.8 cm long, the inner layer ca 1 mm thick, glabrous within.

Additional material examined: BOLIVIA. BENI: junction of Ríos Beni & Madre de Dios, VIII.1886, fl., *Rusby 861* (LE, NY); Río Yata, 10°56'S, 65°33'W, 18.I.1999, *P.J.M. & H. Maas 8690* (K,U). LA PAZ: Murillo, 44.3 km N of dam at Lago Zongo, 1,500 m, 16°05'S, 68°02'W, 19.XII.1982, *Solomon 9182* (MO, NY); Franz Tamayo, 1,017 m, 14°38'51"S, 68°43'29"W, 23.VII.2010, *Villegas et al. 429* (BOLV, LPB, MO, USZ). PANDO: prov. Maruripi, 5 km from Puerto Rico, 17.IX.2000, fl., *Z. Paniagua et al. 698* (LPB, MBM, MO). BRAZIL. AMAZONAS: Reserva Extrativista Canutama, Rio Purus, 29.VIII.2010, *Prata 218* (INPA). RONDÔNIA: Rio Ouro Preto, trib. Rio Pacaas Novas, 19.IX.1923, fl., *Kuhlmann 480* (RB).

This species is distinct from related species by the deeply dentate leaf margins, and the tomentellous exterior of the calyx.

The species is present in upper Rio Madeira region of Bolivian and Brazilian Amazonia. Forests on non-flooded ground.

Caryocar dentatum is listed as rare (R) in Walter & Gillett (1998).

1.8. *Caryocar edule* Casaretto, Nov. Stirp. Bras. Decad. 8: 67. 1844. Fig. 3b
Caryocar barbinerve Miquel, Linnaea 22: 802.1849.
Type: BRAZIL. BAHIA: Ilheus, *Blanchet 3970* (holotype U0000973; isotypes C10009094, G00226259, G00226260, K000432505, P01900576, P01900577, P01900578).
Caryocar crenatum Wittmack, Mart. *Fl. bras.* 12(1): 351 (1886). Type: BRAZIL. RIO DE JANEIRO: São Paulo de Barra, *Riedel 564* (holotype LE).
Type: BRAZIL. RIO DE JANEIRO: fl., *Riedel, Casaretto herbarium No 1948* (holotype: TO).

Tree, young branches glabrous. Leaves trifoliolate; petioles 4–10 cm long, glabrescent, terete; leaflets shortly petiolulate, the terminal petiolule 4–13 mm long, lateral petiolules almost equal to or shorter than the terminal one, petiolules sparsely puberulous soon glabrescent, deeply canaliculate; stipels usually 4, 2 larger than the others, 5–12 mm long, membraneous, recurved, inflated, persistent; laminas oblong, elliptic to ovate-elliptic, slightly asymetrical, subcoriaceous, acuminate at apex, acumen 4–13 mm long, rounded to subcuneate and slightly unequal at base, crenate at margins, glabrous above except for puberulous midrib and primary veins, glabrous beneath except for tomentellous to puberulous midrib and primary veins and their axils, axils hirsute to glabrescent, terminal lamina 7–16 × 4–8.5 cm, the lateral laminas slightly smaller than the terminal one; primary veins 9–12 pairs, plane to prominulous above, prominent beneath; venation prominulous beneath. Peduncles 4–10 cm long, glabrous, terete, sparingly lenticellate. Inflorescences clustered to elongate racemes, 34–35-flowered, the rachis ca

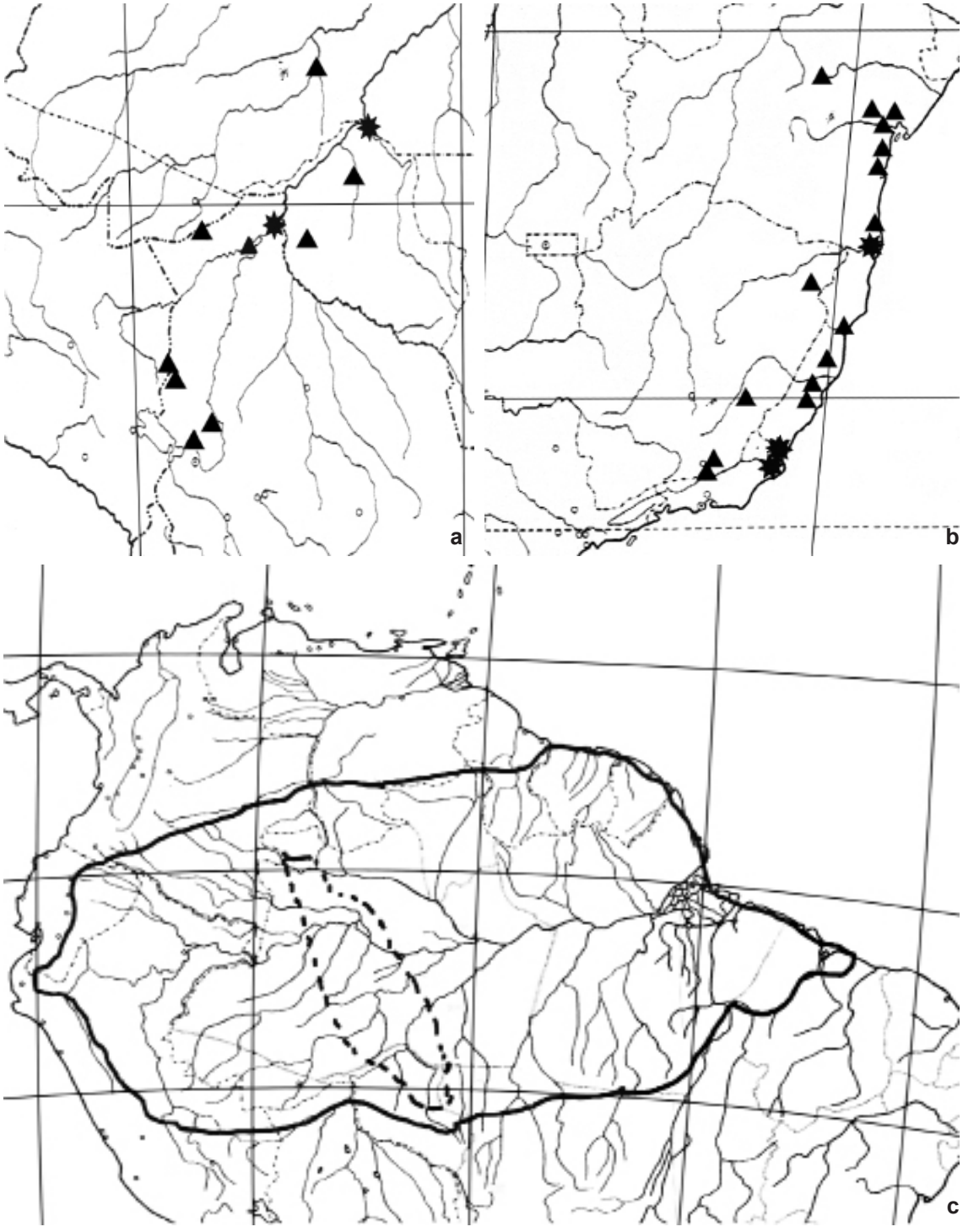

Figure 3 – a-c. Distribution of *Caryocar* species – a. *C. dentatum*, stars = known distribution in 1973; b. *C. edule*, stars = known distribution in 1973; c. solid line = *C. glabrum* subsp. *glabrum*, dotted line = *C. glabrum* subsp. *parviflorum*. (based in Prance & Silva (1973)).

2.5–9 cm long, glabrescent; flowering pedicels 1.4–3.2 cm long, glabrescent; bracteoles minute, membraneous, caducous. Calyx cupuliform, 4–8 mm long, sparsely puberulous on exterior; lobes 5, rounded, the margins ciliolate. Corolla lobes 5, yellow, oblong (seen in bud). Stamens numerous, the filaments (in bud) tuberculate on apical portion, yellow, the anthers small. Ovary globose, 4-locular, glabrous on exterior. Styles filamentous. Fruit globose to slightly ellipsoid, 5-6 cm diam., 1–2-locular, smooth and glabrous on exterior; endocarp covered with long spines.

Additional material examined: BRAZIL. BAHIA: *Sellow 1069* (BM, C, LE, UC, US); Una, Fazenda São Rafael, 12.XII.1968, fl., *dos Santos 302* (CEPEC, K, NY). BRAZIL. MINAS GERAIS: Descoberto, Res. Biol. Represa do Grama, 8.III.2003, fr., *Assis et al. 735* (CESJ). ESPÍRITO SANTO: road Santa Tereza to Nova Lombardia, Sítio Sr. Alcinoades, 4.II.1985, *Peixoto 3431* (NY). Linhares, Reserva CVRD, Est. Bicuba, 23.XII.1981, fl., *Folii 354* (CVRD, INPA, MO, NY). RIO DE JANEIRO: *J.G. Kuhlmann RB 9101* (RB, U). Nova Iguaçú, Res. Biol. Tinguá, Estrada Boa Esperança, 18.I.2002, fl., *Bovini 2148* (CEPEC, MBM).

The fruit is much used for the edible oil and the wood for carpentry.

Caryocar edule is easily distinguished by the 4 stipels, 2 of which are larger, inflated and recurved. The identity of this species has been much confused in the past because the type specimen had not been studied. Wittmack, who obviously did not see the type of *C. edule*, reduced *C. edule* to a variety of *C. glabrum*. All material actually studied by Wittmack and placed by him in *C. glabrum* var *edule* in fact belongs to *C. microcarpum*. Wittmack described the new species *C. crenatum* to accommodate other material which in fact matches the type of *C. edule*. Thus *C. crenatum* is synonymous with *C. edule*. Similarly, *C. barbinerve* is a synonym of *C. edule,* there being no differences between them.

Prance & Silva (1973) attributed the type collection number to Riedel 1948. The collection is by Riedel without number and is number 1948 of the Casaretto herbarium (Delprete *et al.* 2019).

The East coast region of Brazil. Coastal forest and in rocky places beside streams.

Illustrations in Wittmack, Martius *Flora brasiliensis* 12(1) t.70 fig. 2 (1886); t. 69 figs. XII, XIII. (also t. 71 as *C. barbinerve* & t. 72 as *C. crenatum*); Perdiz *et al.* (2012: 112).

Local name: *pequi, pequi preto, pequiá.*

Caryocar edule is listed as vulnerable (V) in Walter & Gillett (1998).

1.9. *Caryocar glabrum* (Aublet) Persoon, Syn. Pl. 2: 84. 1806. Fig. 3c

Souari glabra Aublet, Pl. Guiane 1: 599, *t. 240*. 1775.

Pekea ternata Poiret, Encyc. Méth. 5: 148. 1804, nom illegit.

Rhizobolus saouvari Correa, Ann. Mus. Hist. Nat. Paris 8: 394, *t. 5, f. 2*. 1806., nom. illegit.

Rhizobolus souari Steudel, Nom. Bot. ed. 1. 688. 1824., nom. illegit.

Rhisobolus glaber (Aublet) Correa *ex* Steudel, Nom. Bot. ed. 2. 449. 1841, nom. illegit.

Caryocar coccineum Pilger, Notizbl. Bot. Gart. Berlin 10: 127. 1927. Type: PERU. LORETO: mouth of Río Santiago, *Tessmann 4092* (holotype B, lost; photos, F, MO, NY; lectotype G00226261; isotype S-R-11445).

Caryocar tessmannii Pilger, Notizbl. Bot. Gart. Berlin 10: 126. 1927, syn *C. amygdaliforme* exclusum. Type. PERU. LORETO: Pongo de Manseriche, 1924, *Tessmann 4324* (holotype B, lost; photos, F9700, MO, NY; lectotype, here designated NY00429030).

Caryocar toxiferum Barbosa Rodrigues, Vellosia 1, ed. 1. 11, t. 6. 1888, ed. 2. 11, t. 6(1) (1891). Type. Plate 6 in Vellosia 1, ed. 1 (1888).

Type: FRENCH GUIANA: *Aublet* (isotype BM).

Tree to 50 m tall, usually smaller, the trunk with thick buttresses, the young branches glabrous or sparsely puberulous-glabrescent. Leaves trifoliolate; petioles 3–10 cm long, glabrous or sparsely puberulous-glabrescent terete; leaflets shortly petiolulate, terminal petiole 3–10 mm long, lateral petiolules equal or slightly shorter than the terminal one, petiolules sparsely puberulous, glabrescent, usually shallowly canaliculate; stipels minute, caducous, or rarely larger and persistent; laminas elliptic, oblong-elliptic or ovate-elliptic, slightly asymetrical, acuminate at apex, acumen 5–10 mm long, rounded to subcuneate and unequal at base, entire to slightly crenate at margins, glabrous above, glabrous beneath or with few hairs on midrib and an hirsute mass at junction of midrib with primary veins; the terminal lamina 7.5–15(–18) × 3.5–7(–9) cm, lateral laminas about equal to the terminal one; primary veins 8–10 pairs, more or less plane above, prominent beneath; venation plane to prominulous beneath. Peduncles 2–8.5 cm long, glabrous or sparsely puberulous-glabrescent, terete, lenticellate. Inflorescences of clustered racemes, 10–30-flowered, the rachis 1.5–6.5 cm long, glabrous or sparsely puberulous, lenticellate;

flowering pedicels 1–2.6 cm long, glabrous or sparsely puberulous, ebracteolate. Calyx broadly cupuliform, 7–12 mm long, glabrescent on exterior; lobes 5, rounded, the margins shortly ciliolate. Corolla 1.7–2.5 cm long; lobes 5, slightly unequal, oblong, yellow, sometimes tinted orange. Stamens numerous ca 280, the filaments shortly united at base into a caducous unit, but not into groups, the outer ones 3–6 cm long, red to bright purple, rarely yellow or white, apical portion tuberculate, inner filaments much shorter, 1–1.5 cm long, tuberculate entire length; anthers small. Ovary globose, 4-locular, glabrous on exterior. Styles 4, 4–5 cm long, glabrous, filamentous. Fruit ellipsoid-globose, 1- or 2-locular (rarely to 4-locular), 5–6 cm long, 5–8 cm broad; exocarp glabrous, crustaceous; pericarp thick, fleshy, remaining attached to mesocarp; mesocarp fleshy, enveloping endocarp spines but detaching from them easily; endocarp of numerous fine spines 5–15 mm long and a hard woody interior ca 2 mm thick, glabrous within. Germination hypogeal.

Key to the subspecies of *Caryocar glabrum*

1. Stipels caducous; calyx 8–12 mm long; stamens 5–6 cm long..... ..... 1.9.1. *Caryocar glabrum* subsp. *glabrum*
1'. Stipels persistent; calyx ca 7 mm long; stamens 3–4.5 cm long.
   2. Primary leaf veins with glabrous axils; inflorescence rachis 2–3 cm long..... ..... 1.9.2. *Caryocar glabrum* subsp. *parviflorum*
   2'. Primary leaf veins with barbate axils; inflorescence rachis ca 7 cm long..... ..... 1.9.3. *Caryocar glabrum* subsp. *album*

1.9.1. *Caryocar glabrum* subsp. ***glabrum***.

Fig. 3c

Additional material examined: VENEZUELA. BOLÍVAR: *Steyermark 75635* (NY, VEN). AMAZONAS: Maroa, Rio Guainía, 16.II.1942, fr., *Ll. Williams 14377* (F, G, NY, US, VEN); Tributary of Río Cunucunuma, N flank of Cerro Duida, 03°43'N, 65°39'W, IV.1990, fl., *Fernández 7635* (K, MO). GUYANA. Akarai Mts, between Mapuera and Shodikar Creek, 19.I.1938, fl., *A.C. Smith 2727* (A, F, G, K, MO, NY, P, S, U, US); Potaro-Siparuni, Iwokrama Reserve, Karupukaro, 800 m, 04º19'N, 58º48'W, 25.III.1997, fr., *Mori 24595* (K, NY). SURINAME. Near Moengo Tapoe, 29.X.1948, fl., *Lanjouw & Lindeman 980* (IAN, K, NY, U); Kamoa River, near Toucan Mt. 01º32'N, 58º50'W, 15.IX.1989 *Jansen-Jacobs et al. 1607* (K, U). FRENCH GUIANA. Tres Saltos, Rio Oyapoque, 13.IX.1960, fl., *Irwin et al. 48218* (F, IAN, M, MG, NY, S, U, US); Montagne de la Trinité NE summit, 400 m, 4.II.1984, fr., *Granville 6501* (CAY, K, MG, NY, U). BOLIVIA. PANDO: S Bank Rio Abunã, 5 km above mouth, 14.XI.1968, fl., *Prance et al. 8436* (INPA, K, MG, MO, NY, US). COLOMBIA. AMAZONAS: Tarapacá, 03°02'S, 70°00'W, 100 m, 8.VII.1992, *Rudas et al. 4948* (MO). ANTIOQUIA: Zaragoza mun., Corr. de Providencia above confluence Quebrada Tiranu and Río Anorí, 600-700 m, 11.II.1971, *Soejarto & Villa 2793* (COL, MO); mun. San Carlos, Alto de Samaná, vereda Miraflores, 750-890 m, 06º05'N, 74º50'W, 26.X.1989, fr., *Callejas et al. 8610* (K). CAQUETÁ: mun. Belén de los Andaquíess, Alto Sarabando, 1.43055, -75.88777, 26.III.2013, fr., *Cárdenas 43335* (COAH, MO). VAUPÉS: Río Apaporis, Sorotama between Río Pacoa & Río Kananarí, 20.VIII.1951, fl., *Schultes & Cabrera 13600* (BM, BR, C, COL, S, U, UC). PERU. AMAZONAS: Bagua, -5.46722, -78.386380, 20.XII.2001, fl., *Vásquez et al. 27544* (MO). CUSCO: Paucartambo, 780 m. -12.89805, -72.37361, 1.V.2003, *Huamantupa & Quispe 2948* (CUZ, MO). HUÁNUCO: Puerto Inca, 450 m, -9.69166, -75.55833, 4.III.2006 -10.933333, -75.25000, 14.IV.1984, fr., *Smith & Brack 6934* (K, MO). LORETO: Maynas, Gauzo Azul, 28.XI.1961, fl., *V. Arostegui 11* (F, G, NY, US, WIS). PASCO: Oxapampa, 430 m, -10.37666, -75.01166, 22.X.2005, fl., *Monteagudo et al. 10985* (HUT, MO, USM). PASCO: Oxapampa, Dist. Palcazú, Res. Comunal Yanesha-Sector Azulis, 10°29'09"S, 75°06'46"W, 670 m, 24.II.2004, fr., *Vásquez et al. 29542* (K, MO). ECUADOR. MORONA-SANTIAGO: Limón Indanza, -3.059444, -78.24583, 1,150 m, 19.XII.2005, *Morales et al. 1541* (MO, QCNE). NAPO: Río Bueno, Santa Rosa, 9.V.1972 (fl only), *Lugo 2186* (GB, NY); Orellana Cantón, Tiputini Biodiv. Station, 00°38'S, 76°10'W, 250 m, II.1998, fl., *Pitman & Delinks 3085* (K, MO). PASTAZA: Río Curiacu, 8 km W of Puerto Sarayacu, 19.X.1974, fl., *Lugo 4276* (BG, NY). SUCUMBIOS: Cascales. 250 m, 00°00', 77°45'W, 5.V.1997, *Freire et al. 2264* (MO, QCNE). ZAMORA-CHINCHIPE: Nangaritza, -4.140833, -78.64555, 22.IV.2006, fl., *Neill et al. 15148* (ECUAMZ, MO, QCNE). BRAZIL. ACRE: 2-4 km W of Cruzeiro do Sul, X.1966, fl., *Prance et al. 2740* (INPA, K, MG, MO, NY, US). AMAZONAS: near mouth of Rio Embira, trib. of Rio Tarauacá, 07°30'S, 70°15'W, 14.VI.1933, fl., *Krukoff 4812* (A, BM, F, G, K, M, MO, NY, S, U, UC, US). Tefé, Vila Nogueira,

lago Tefé, 13.X.1982, fl., *Amaral et al. 58* (INPA, K). AMAPÁ: 00°10'N, 61°37'W, 12.IX.1983, *Mori 16100* (INPA, MO, NY). PARÁ: Belém, Bosque Municipal, 30.IX.1944, fl., *Ducke 1639* (IAN, MG, NY, US). RONDÔNIA: UHE Jirau, BR-364, W of Embaúba, -9.52722, -64.81722, 9.X.2012, fl., *Simon 1685* (INPA, K). MATO GROSSO: Vila Bela da Santíssima Trindade, 4 km S of Rondônia boundary, 12º54'S, 60º02'W, 3.XI.1985, fl., *Thomas et al. 4798* (INPA, K, NY); mun. Novo Mundo, SE of Parque Estadual Cristalino, 386 m, 09º34'59"S, 55º11'59"W, 27.I.2008, fr., *Sasaki 1991* (K, SPF). MARANHÃO: Ka'apor Indian Reserve, 4 km NW Urutawy, Monção, 5.II.1985, *Balée 4110* (NY).

The kernel of the fruit is eaten by natives throughout its range. The epicarp of the fruit is used as a fish poison in the upper Amazon in Colombia, Brazil and Venezuela (Kawanishi *et al.* 1986), and by the Makú Indians on the Rio Uneuixi (Prance 1972a). The wood is used in boat construction throughout Amazonia. The inner bark is used for washing hair and clothes because of the saponin content and hence the local name soapwood.

Wittmack (1886) divided *C. glabrum* into 3 varieties, var *pilosum* belongs within *C. microcarpum* rather than *C. glabrum*. Likewise, the majority of the material placed by Wittmack in his var. *edule* belongs to *C. microcarpum*. Variety *edule* was based on the species *C. edule* Casar. which is quite distinct from *C. microcarpum*.

The taxon is distributed in Guianas and northern Amazonia from Colombia, Peru and Venezuela to eastern Pará, Brazil. Forests on non-flooded ground.

Illustrations in Wittmack, Martius *Flora brasiliensis* 12(1) t. 70 fig. 1 (1886); Prance (1998, fig. 118).

Local names: Colombia: *Haw, ho'shoo* (Puinave), *e-ko* (Barasana), *kön* (Kubeo); Venezuela: *jigua, jigua barbasco*; Suriname: *aloekoemarirang, sawarie, sopohoedoe*; (Paramaka); Peru: *almendra, almendro*; Brazil: *Pequirana, pûrsh* (*makú*)*, piquiarana-vermelha, piquiá da areia, piquiá-da-areia; piquiarana da terra, piquiarana-da-terra, piquiá-rana da terra firme, saouari;* English*: soapwood*.

Caryocar glabrum subsp. *glabrum* is Least concern (LC).

1.9.2. ***Caryocar glabrum*** subsp. ***parviflorum*** (A.C. Smith) Prance & Silva, Fl. Neotrop. Monogr. 12: 43. 1973. Fig. 3c
Caryocar parviflorum A. C. Smith, J. Arnold Arb. 20: 298.1939. Stipels small but persistent; calyx ca 7 mm long, stamens 3–4.5 mm long.
Type: BRAZIL: AMAZONAS, Humaitá, Rio Livramento, X-XI.1934, *Krukoff 6599* (holotype NY00429027; isotypes A00062686, BM000603037, BR0000006986285, FV0053252, G00226263, K000432518, L1055829, MO-279614, S-R-11455, U0000975, US01879840, US00113826, USw7805; WIS00000716MAD).
Additional material examined: BRAZIL. AMAZONAS: Humaitá, Três Casas, IX-X.1934, fl., *Krukoff 6438* (A, BM, BR, F, G, K, LE, MO, NY, S, U, US); Rio Makira, 3.IX.1923, fl., *R.B. Kuhlmann 17887* (K, RB). RONDÔNIA: Tabajara, Rio Machado, XI-XII.1931, fl., *Krukoff 1381* (A, BM, F, G, K, MO, NY, P, S, U, UC, US).

Caryocar glabrum subsp. *parviflorum* is present in Southern central parts of Brazilian Amazonia. Forests on non-flooded ground.

1.9.3. *Caryocar glabrum* subsp. ***album*** Prance & Silva, Fl. Neotrop. Monogr. 12: 43 1973. Axils of the primary veins barbate; inflorescence rachis 6-7 cm long; filaments white.
Type: GUYANA. Upper Mazaruni River, Morabukea forest, Kamarang Station, 26.X.1951, fl., *Maguire & Fanshawe 32326* (holotype NY429014; isotypes INPA, K000432500, MO-279618, P01900569, S-R-11448, U0124054, VEN100539).
Additional material examined: GUYANA. CUYUNI-MAZARUNI: Paruima, 0.2-0.2 km E of Ararata, 780 m, 05º49'N, 61º08'W, 5.VII.1997, fl., *Clarke 5386* (K, US). BRAZIL. AMAZONAS: Rio Cuieiras below Aracá 00º48'N, 63º21'W, 13.VII.1985, fr., *Prance et al. 29531* (INPA, K, SP).

Caryocar glabrum subsp. *album* is listed as Endangered (E) in Walter & Gillett, IUCN (1998).

1.10. *Caryocar gracile* Wittmack, Mart. *Fl. bras.* 12(1): 350.1886. Fig. 4a
Caryocar krukovii Gilly, Trop. Woods 72: 17. 1942.
Type: BRAZIL. AMAZONAS: mun. São Paulo de Olivença, Creek Belém, X-XII.1936, *Krukoff 8838* (holotype NY429020; isotypes A00062684, BM000603036, BR0000005314553, F V0053248, G00226266, K000432502, LE, P01900566, S-R-11449, U0000976, US01879847).
Type: BRAZIL. AMAZONAS: Rio Uaupés, Panuré, X.1852-I.1853, *Spruce 2550* (holotype B, lost; photos, F, MO; lectotype of Prance & Silva 1973, OXF; isolectotypes BM000603033, C10009096, CGE, E00326634, F V0053247, G00226264, G00226265, GH00062683, GOET000557, K000432503, K000432504, LD2071354, LE, MPU014411, NY429017,

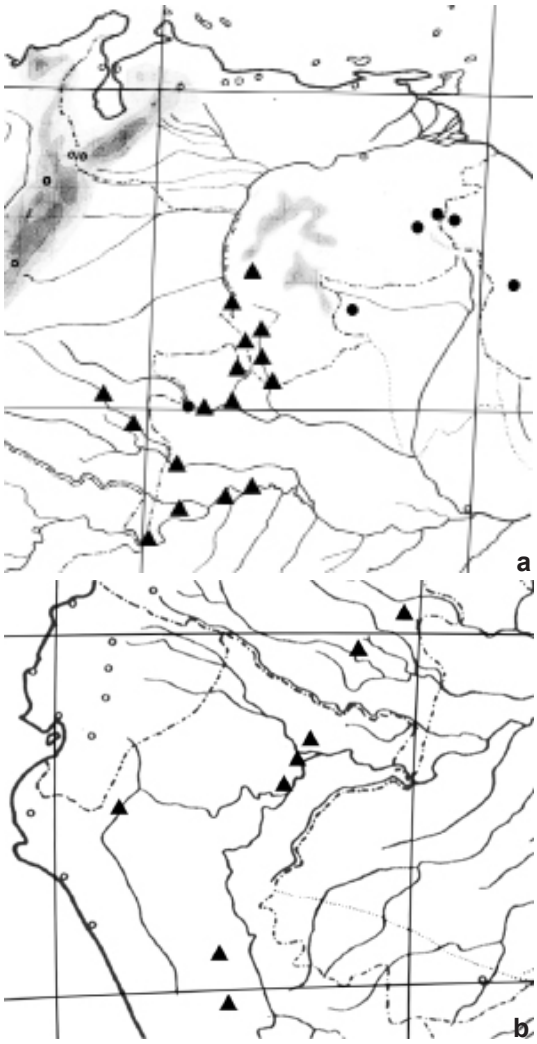

Figure 4 – a-d. Distribution of *Caryocar* species – a. triangles = *C. gracile*, circles = *C. montanum*; b. *C. harlingii*. (based in Prance & Silva (1973)).

NY429018, P01900568, RB00538050).

Tree to 30 m tall, the young branches glabrous. Leaves trifoliolate; petioles 2–5.5 cm long, glabrous, terete; leaflets shortly petiolulate, terminal petiolule 0.3–1.4 cm long, lateral petiolules slightly shorter than the terminal one, petiolules glabrous, terete to shallowly canaliculate; stipels absent; laminas oblong to oblong-elliptic, acuminate at apex, acumen 1–5 mm long, rounded to subcuneate at base, often slightly unequal, crenulate to entire at margins, glabrous above, glabrous beneath or with few villous hairs at junction between primary veins and midrib, terminal lamina 4.5–12.5 × 2.5–7 cm, lateral laminas equal or smaller than the terminal one; primary veins 6–9 pairs, prominulous above, prominent beneath; venation plane to prominulous beneath. Peduncles 4–6.5 cm long, glabrous, terete, lenticellate. Inflorescences elongate racemes, the rachis 6–14 cm long, glabrous, lenticellate; flowering pedicels 7–17 mm long, glabrous, ebracteolate. Calyx cupuliform, 4–6 mm long, glabrous on exterior, the lobes 5, rounded, the margins ciliate. Corolla 1–1.3 cm long, the lobes 5, elliptic, rose-pink. Stamens numerous, over 400 average number 509, the filaments shortly united at base only, but not in groups, not caducous, white or part distinctly tuberculate, the innermost only 0.5 cm long, with all intermediate lengths in between, the smallest tuberculate most of length, the anthers small. Ovary globose, glabrous, 3(–4)-locular. Styles 2–3, filamentous, exceeding filaments in length, glabrous. Fruit with endocarp ca 3.5 cm long, 4.5 cm broad, the exterior of endocarp with numerous spinous protrusions, the spines longer and thinner towards the base, the inner portion ca 1.5 mm thick, very hard, glabrous within.

Additional material examined: VENEZUELA. AMAZONAS: Río Yatuá, Neblina camp 3, 30.XII.1957, fl., *Maguire et al. 41933* (M, NY, RB, S, US, VEN); lower slopes of Cerro de la Neblina, 700-800 m, 30.XII.1957, fl., *Maguire et al. 42533* (K, NY). Río Varia, 01°25'N, 66°24'W, 90 m, IV.1991, fl., *Velazco 1775* (K, MO); Dpto Atabapo, Río Caname, 03º41'N, 66º27'W, 95 m, XI.1989, *Yanez 61* (K). COLOMBIA. CAQUETÁ: Río Caquetá, Cupatí cataracts, 15.XI.1923, *Ducke MG 12253* (F, G, MG, P, RB, S, U, US). Guainía, *Weiss & Schmidt* (NY). Vaupés, Río Kananari, trib. Apaporis, Cerro Isibukuri, 29.IX.1951, *Schultes & Cabrera 14688* (BM, COL, U). BRAZIL. AMAZONAS: Foz de Jutaí, 20.XI.1927, *Ducke RB 21092* (F, G, INPA, K, P, RB, S, U, US); 4 km from Estrada de Breu, Jutaí, -2.74667, -66.76670, 29.X.1986, fl., *Cid Ferreira et al. 8330* (INPA, MBM, MO, NY, US). Novo Japurá, between Tamandaré and Manguarí, 12.XI.1982, *Cid Ferreira 3605* (INPA, MO, NY, US).

The leaves of *Caryocar gracile* are used as a poison for killing dogs by the Tukanos Indians (Kawanishi *et al.* 1986). The leaves are mashed into a paste and eaten by the dogs since the Indians believe that dogs should have a slow death and with this species it takes up to a week for a dog to die.

Wittmack in the protolog of this species cites Spruce 1872 from Manaus under this species with a question mark. That collection is actually of *C. microcarpum* and so is not cited here as syntype of *C. gracile*.

The species is present in Western Amazonian Brazil and adjacent Colombia and Venezuela. Forest on non-flooded ground.

Local names: Brazil: *Pequi rosada*; Venezuela: *jigua comestible*.

Caryocar gracile is Least concern (LC) in IUCN red list.

1.11. *Caryocar harlingii* Prance & F. Encarnación, Opera Botanica 92: 182. 1987.
Type: PERU. LORETO: Río Ucayalí, Arboretum Jenaro Herrera, 16.XI.1984, 73°45'W, 04°55'S, *Prance 29333* (holotype NY00429019; isotype MO-1252569). Fig. 4b

Tree to 30 m tall, young branches glabrous. Leaves trifoliolate; stipules 15–20 mm long, concave, deciduous; petioles 2.8–10 cm long; terminal petiolule 7–15 mm long, lateral petiolules 4–10 mm long, petiolules glabrous or sparsely puberulous, canaliculate; stipels absent; laminas oblong-elliptic, slightly asymmetric, glabrous above, glabrous beneath except for hirsute axils of veins, apex abruptly acuminate, acumen 5–20 mm long, subcuneate at base, margins slightly crenulate; terminal lamina 8.5–16 × 4.5–8.5 cm, lateral laminae smaller; primary veins 10–12 pairs, plane above, prominent beneath. Peduncles 5–15 cm long, glabrous, square in cross-section, not lenticellate. Inflorescences clustered racemes with 15–20 flowers, the rachis glabrous; pedicels 15–20 mm long, not lenticellate. Calyx broadly cupuliform, 7–9 mm long, glabrous on exterior, ebracteolate, bracteoles inserted below pedicels, caducous. Petals 5, oblong, 15–20 mm long, yellow. Stamens numerous; filaments slightly connate at base for 3–4 mm, yellow. Ovary globose, 4-locular, glabrous on exterior. Style filamentose, glabrous. Fruit ovoid, 5–6 cm diam; mesocarp fleshy; endocarp spiny on exterior.

Additional material examined: COLOMBIA. AMAZONAS: La Chorrera, Río Igara-Paraná, *Sastre 32762* (NY, P). VAUPÉS: Yapu, alto Río Papuri, *Patmore & Dufour 167* (NY); Río Apaporis, raudal de Jirijirimo, 1951, *Schultes 13497* (NY). PERU. AMAZONAS: Bagua, Comunidad de Yamayakat, 350 m, -5.05666, -78.33805, 8.XI.1997, fl., *Rojas 538* (MO). LORETO: Prov. Requena, Arboretum Jenaro Herrera, *Spichiger & Encarnación 1079* (G, NY).

For a table of differences between this species and *C. glabrum* see Prance (1987).

The species is distributed in Amazonian Colombia and Peru. Non-flooded rainforest.

Illustration in Prance (1987).

1.12. *Caryocar microcarpum* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 133. 1925.
Caryocar glabrum var. *edule* Wittmack, Mart. *Fl. bras.* 12(1): 349. 1886, pro parte, syn. *C. edule* Casaretto exclusum.
Caryocar glabrum var. *pilosum* Wittmack, Mart. *Fl. bras.* 12(1): 349. 1886. Type: BRAZIL. PARÁ: Santarém, *Spruce* (Apr 1850) (holotype LE; isotypes G00226268, GH00062682, NY00429015, NY00429016, S-R-11447).
Caryocar butyrosum sensu Stahel (non Aublet), Ser. Overdr. Landbouwproefstation, Suriname 7: 5. 1935.
Caryocar riparium A.C. Smith, Lloydia 2: 195. 1939. Type: GUYANA. Kuyuwini River, 150 miles from mouth, *A.C. Smith 3034* (holotype NY00429029; isotypes A00062687, A00062688, FV0053253, G00226239, K000432519, K000432520, NY00429028, P01900564, S-R-11456, U0000977, US00113828, WIS00000717MAD, WIS00000718MAD).
Type: BRAZIL. PARÁ: Belém, 4.X.1923, fl., *Ducke RB 17835* (lectotype RB; isolectotypes F0BN009699, G0022627, K000432515, P01900565: photos of B lost, F, MO, NY). Probable isotypes *Ducke*, 4.X.1923, (RB 00538052, RB00538047). Syntype: PARÁ: Belém, *MG Ducke 15500*, (MG, US00110235, frag, V0053250F, NY00429022). Fig. 5

Tree to 25 m tall, often smaller, the trunk not buttressed, the young branches glabrous, lenticellate. Leaves trifoliolate; petioles 2–10 cm long, terete, glabrescent; leaflets shortly petiolulate, terminal petiolule 1–5 mm long, lateral petiolules equal to or slightly smaller than the terminal one, petiolules puberulous, glabrescent with age terete to shallowly canaliculate; stipels conduplicate-cylindrical, strongly recurved 2–5 mm long, persistent; laminas oblong, usually slightly asymetrical, acuminate at apex, the acumen 6–15 cm long, subcuneate or cuneate at base, entire or weakly crenulate at margins, glabrous above, entirely glabrous beneath or the midrib and primary veins sparsely pubescent the terminal lamina 5–15 × 2–6.5 cm, lateral laminas usually smaller than the terminal one; primary veins 10–14 pairs, prominulous above, prominent beneath; venation plane or prominulous beneath. Peduncles 5–15 mm long, glabrous or sparsely puberulous-glabrescent, terete, not conspicuously lenticellate. Inflorescences clustered racemes, 10–25-flowered; rachis 1–5 cm long, glabrous or minutely puberulous, with 2 membraneous early caducous bracteoles. Calyx cupuliform, 5–6 mm

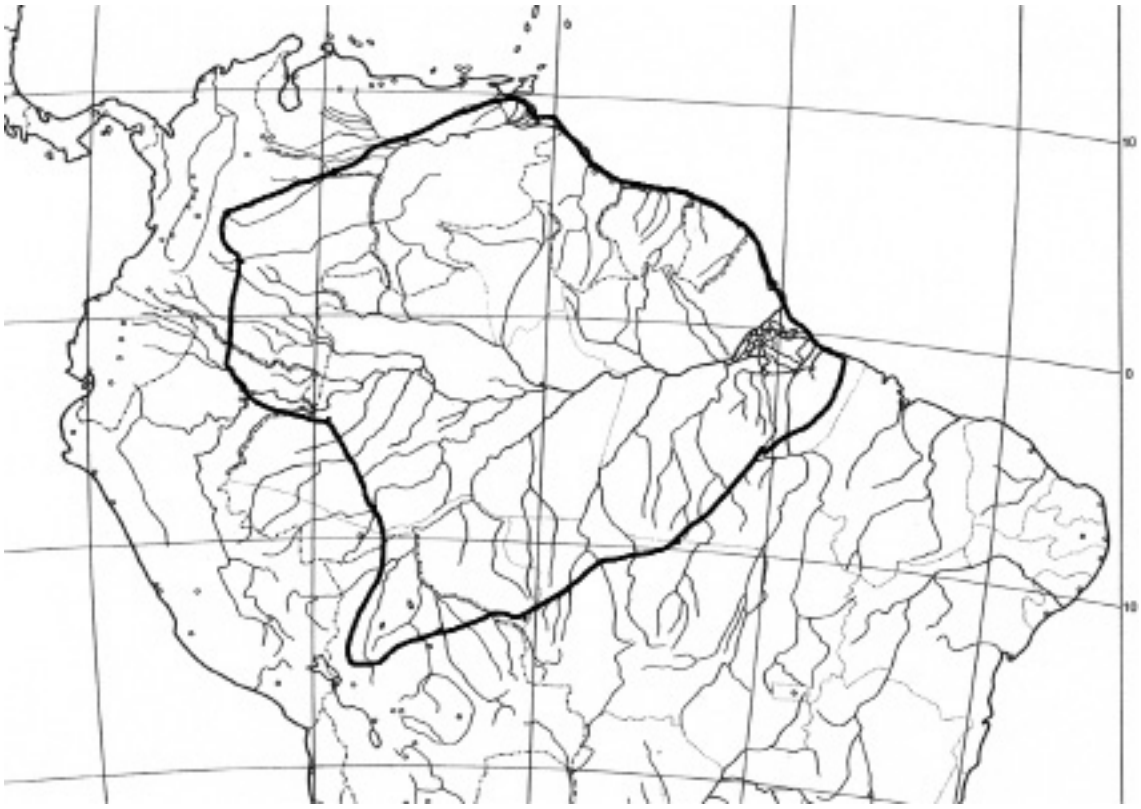

Figure 5 – Distribution of *Caryocar microcarpum*, almost unchanged from 1973.

long, glabrous or minutely puberulous on exterior; lobes 5, rounded, the margins ciliolate. Corolla 1.8–2.5 cm long; lobes 5, oblong, yellowish white. Stamens numerous, ca 55–150, the filaments shortly united at base into a caducous ring, but not into groups, of two distinct lengths, the largest ca 85, 5–7 cm long, most frequently white or yellow, but sometimes rose to bright reddish-purple, apical portion tuberculate, the smallest ca 35, 1 cm long, tuberculate for entire length, many sterile; anthers small. Ovary globose, 4-locular, glabrous on exterior. Styles 3–4, ca 6 mm long, filamentous, glabrous. Fruit ovoid-reniform to ellipsoid, 2–3.5 cm long, 2.5–3 cm broad, usually 1- or 2-locular, rarely 3-locular; exocarp smooth, glabrous, not crustaceous; pericarp thick, fleshy, remaining attached to mesocarp; mesocarp thick, fleshy, enveloping endocarp spines; the stone reniform; endocarp with a short-spined exterior, the spines 2–4 mm long, irregular, the inner layer very thin, ca 0.4 mm thick, hard, glabrous within. Germination hypogeal, the first leaves opposite. 2n = 46

Additional material examined: FRENCH GUIANA. Crique Gabaret, between mouth and Crique Mérignan, Basin of Oiapoque, 12.IV.1988, fr., *Granville 10234* (CAY, INPA). Sinnamary, 17.I.1991, fl., *Prévost & Sabatier 3000* (CAY, K, NY, U). GUYANA. Demerara-Berbice, Essequibo R, 2-4 km from Bartica Is, 6.41666, -58.58333, 31.III.1993, fl. and fr., *Henkel et al. 1789* (K, MO); NW Dist., Waini R., IV.1923, fr., *De La Cruz 3814* (F, GH, MO, NY, UC, US); Rupununi, Kanunku Mts, Puwib R. 80-100 m, 3.11666, -59,43333, 18.II.1985, fr., *Jansen-Jacobs et al. 290* (K, MO, U). SURINAME. Mt. Bakhuis, between Kabelebo & Coppename R., II.1965, fl., *Florschütz & Maas 2760* (F, NY, U, UC); Nickerie River, Blanche Marie Falls, 50 m, 04º45'30"N, 56º52'40"W, 6.II.1998, fl., *Evans & Peckham 2789* (K, MO). VENEZUELA. APURE: Dist Pedro Camejo, Morichal de La Madera, near Río Meta, 06°11'N, 68°49'W, 70 m, 16-18.II.1978, fl., *Davidse & González 14202* (MO, NY). AMAZONAS: San Fernando de Atabapo, I.1942, fl., *Ll. Williams 13846* (F, NY, US, VEN); Dept. Atabapo, Río Ocamo, 03°03'N, 67°29'W, 270 m, I.1990, *Fernandez 6671*(K, PORT). BOLÍVAR: Río Parguaza, below El Carmen, 50 km from mouth, XII.1955, fl., *Wurdack & Monachino 40946* (F, G, GH, IAN, K, NY, S, U, UC, US, VEN); Mun. Sucre, margin of Río Ariza, 06°38'N, 64°28'W, 275 m, V.1990, *Delgado 982* (K, PORT). DELTA AMACURO: C. Winipuina, VIII.1954, fl., *Gines 5010* (US). BOLIVIA. BENI: Prov.

Vaca Diez, 17 km S. of Riberalta, 11°08'S, 66°06'W, 18.XI.1989, fl., *Daly et al. 6251* (K, MO, NY). LA PAZ: S. Yungas, San Bartolome, near Calisaya, 1936, fr., *Krukoff 10402* (A, F, G, K, LPB, MO, NY, S, U, UC, US). COLOMBIA. AMAZONAS: Resguardo Aduche, Quebrada Aduche, -0.65000, -72.31666, 1.XII.1993, fl., *Cárdenas & Andoque 4298* (COAH, MO)). CAQUETÁ: Solano, Bocas del Yavillaré, 250 m, -0.007777, -72.17472, 20.XI.1995, fr., *Cárdenas et al. 6825* (COAH, MO). META: La Macarena, Caño Cafre, 300 m, 19.V.1985, fr., *Hurtado 78* (MO). VAUPÉS: Bocas del Carurú, 26.IX.1939, fl., *Cuatrecasas 7041* (COL, F, US). VICHADA: PN N, El Tuparro, Caño Hormiga, 6 km N of El Tapón, 05°11'N, 69°09'W, 21.III.1985, fr., *Zarucchi & Barbosa 3803 (*MO, NY). PERU. LORETO: Maynas Prov., Santa Maria de Nanay, Mishana, 03°55'S, 73°35'W, 2.X.1990, fl., *Pipoly et al. 12728* (K, MO, NY). BRAZIL. ACRE: Acrelândia, 108 km E of Rio Branco, 10º00'37"S, 66º46'14"W, 3.X.2003, fr., *Acevedo-Rodriguez et al. 13637* (K, NY). AMAPÁ: Rio Oiapoque, 1.II.1950, fl., *Fróes 25790* (IAN). AMAZONAS: Manaus, Igarapé do Crespo, 13.II.1943, fl., *Ducke 1184* (IAN, K, MG, MO, NY, UC, US). PARÁ: Belém, *MG Ducke 15500*, (MG, US00110235, frag, V0053250F, NY00429022); mun. Oriximiná, Campos de Ariramba margin of Rio Jaramacarú, 8.VI.1980, fr., *Martinelli 6873* (K, MO, NY). RONDÔNIA: Rio Jamari, Igarapé Japim a Lagoa de Feijol, Porto Velho, 13.VIII.1987, fl., *Mattos 149* (INPA). RORAIMA: Canta Galo, Mucajaí, 2.I.1967, fl., *Prance et al. 4042* (INPA, K, MG, NY, US). BRAZIL. MATO GROSSO: Rio Aripuanã, Aripuanã, 14.X.1973, fl., *Berg P18529* (INPA, NY). Novo Mundo, Parque Estadual Cristalino, 264 m, 09º26'44"S, 55º50'31"W, 8.II.2008, fr., *Zappi 1104* (HERBAM, K, SPF, MO, NY).

The kernel of the fruit is eaten, but not as much as in other species; the pericarp of the fruit is used as a fish poison in the upper Rio Negro region and in Colombia and Venezuela (Kawanishi *et al.* 1986). The leaves are crushed and used as a substitute for soap by natives of Suriname, French Guiana and parts of Brazil.

The species is find in Guianas and northern Amazonia from Peru, Loreto to Brazil, Pará, also collected in cultivation in the Lesser Antilles. Periodically flooded forest.

Illustrations in Prance & Silva (1973); Prance (1998, fig. 119).

Local names: Colombia: *kun-kuj, ku* (Kubeo); Venezuela: *barbasco, cujón de verraco*, *jigua*, *jigua orillera, jigua verde, mabari-takari* (Arekuna); Guyana: *kula* (Arawak), *bats sawari, water sawari*; Suriname: *aloekoemali, ebencoro, koelo, kula* (Arawak), *kobo, sopohoedoe*; French Guiana: *chawari, souari*, *kassagnan* (Paramaka); Peru: *almendra, almendra de bajo*; Brazil: *piquiarana, piquiarana de várzea, piquiarana de igapó.*

Caryocar microcarpum is listed as Least concern (LC).

1.13. ***Caryocar montanum*** Prance, Mem. N. Y. Bot. Gard. 23:128. 1972.

Type: VENEZUELA. BOLIVAR: Tirepón-tepuí, Chimantá Massif, 1,200-1,250 m, 7.I.1953, fl., *Wurdack 34050*; holotype: NY00429023; isotypes: INPA 28446, MO-279615, US00110236. Paratypes: Río Icaburu, 280° from the source of the Río Hacha, 850 m, 12.I.1956, *Bernardi 2881* (NY); RORAIMA: upper slopes of Serra Surucucus, 1,700 m, 15.II.1969, fl., *Prance et al 9931* (INPA, K, M, MG, NY, S, US, VEN). Fig. 4a

Tree to 30 m tall, young branches glabrous. Leaves trifoliolate; petioles 3.5–7.5 cm long, sparsely puberulous-glabrescent or glabrous, terete; leaflets shortly petiolulate, terminal petiolule 8–17 mm long, lateral petiolules equal or slightly shorter than the terminal one, petiolules glabrous or sparsely pubescent-glabrescent, canaliculate; stipels absent; laminas oblong to oblong-elliptic, usually slightly asymetrical, acuminate at apex, acumen 6–15 mm long, cuneate to subcuneate and unequal at base, entire or weakly crenulate at margins, glabrous above, glabrous beneath or with a hirsute mass in the axils of the primary veins and a few hairs on the midrib and veins, usually slightly papillose beneath, the terminal lamina 8.5–15 × 4–7 cm, lateral laminas slightly smaller than the terminal one; primary veins 8–9 pairs, plane above, prominent beneath; venation plane to prominulous beneath. Peduncles 6–13 cm long, glabrous, with small lenticels but not crustaceous, terete. Inflorescences clustered racemes, 20–28-flowered, rachis glabrous or sparsely puberulous; flowering pedicels 2.3–3.1 cm long, glabrous, not crustaceous, ebracteolate but with 2 caducous membraneous bracteoles at junction with rachis. Calyx broadly cupuliform, 8–11 mm long, glabrescent on exterior; lobes 5, rounded, the margins ciliate. Corolla 2.2–2.6 mm long; lobes 5, oblong, greenish-yellow. Stamens numerous; filaments shortly united at base, into a single caducous unit, but not into groups, of two lengths, the larger ones ca 110, 4–5.5 cm long, yellow, only the apical portion tuberculate, the smaller ones ca 22, ca 1 cm long, tuberculate entire length, with smaller anthers. Ovary globose,

(3–)4-locular, glabrous on exterior. Styles 4, glabrous, filamentous. Fruit not seen.

Additional material examined: GUYANA. POTARO-SIPARUNI REGION: Iwokrama Reserve, 04°20'N, 58°50'W, 600-800 m, 22.XI.1995, fl., *Clarke 579* (K, U, US); Slopes of Mt. Roraima, Arabupu, 4,600 feet, 23.XII.1938, fl., *For. Dep. 2833* (K). VENEZUELA. BOLÍVAR: Ptaritepui, 1,585 m, 10.XI.1944, *Steyermark 59999* (F, NY, US, VEN); Río Icaburu, 280° from the source of the Río Hacha, 850 m, 12.I.1956, *Bernardi 2881* (NY). BRAZIL. AMAZONAS: Rio Tiquié, Rio Negro, São Gabriel da Cachoeira, 13.XII.1975, fl., *Coêlho 254* (INPA). RORAIMA: upper slopes of Serra Surucucus, 1,700 m, 15.II.1969, fl., *Prance et al. 9931* (INPA, K, M, MG, NY, S, US, VEN); Indian trail from Siurucucus to Uaicá between Mayoobtedi and Botamatatedi, about 03°N, 8.II.1971, fl., *Prance et al. 13551* (INPA, NY, U, US).

This species is closest to *C. glabrum* but differs in the longer, thinner pedicels which are not crustaceously lenticellate, the greater length of the terminal petiolule, the papillose lower surface of the leaves, and the white filaments. It grows at a higher altitude than *C. glabrum* and appears to be confined to the slopes of sandstone mountains.

The species is present in Guayana Highland of Venezuela and adjacent Guyana and Brazil. Forests on slopes between 1,000 and 2,000 m.

Illustrations in Prance (1972b); Prance & Silva (1973).

Caryocar montanum is listed as rare (R) in Walter & Gillett (1998).

1.14. *Caryocar nuciferum* Linnaeus, Mantissa plantarum 2: 247. 1771. Fig. 6a

Pekea tuberculosa Aublet, Pl. Guiane 1: 537, *t. 239.* 1775, pro parte quoad fructus tantum.

Rhizobalus tuberculosus (Aublet) Gmelin, Linn. Syst. Nat. ed. 13. 2(1): 840.1789, pro parte.

Rhizobalus pekea Gaertner, Fruct. 2: 92, *t. 98*. 1790, pro parte, nom illegit.

Caryocar tomentosum Willdenow, Linn. Sp. Pl. ed. 4. 2: 1244. 1799, pro parte, nom illegit.

Amygdala guayanensis Clusius, Exoticorum 27, *t. 1*. 1605, nom illegit; Bauhin, Hist. Pl, 1: 329 (1650); Plunkenet, Phytographia *t. 323*. 1799.

Type: GUYANA. Essequibo & Berbice *F. Allamand* (not seen); Neotype, SURINAME: Saramaca, km 25 of railway, 7.XII.1943, fl. and fr., Woodherbarium, *Stahel 195* (Neotype U1191093, U004120302, here designated; isoneotypes A, NY, USw13001, WAG1220168).

Tree to 45 m tall, the trunk buttressed (ter Steege *et al.* 1997), young branches glabrous. Leaves trifoliolate, petioles 4–9(–15) cm long, terete to flattened, glabrous; leaflets petiolulate, terminal petiolule 7–20 mm long, lateral petiolules about equal to the centre one; petiolules glabrous, shallowly canaliculate; stipels absent; laminas elliptic, acuminate at apex, acumen 5–15 mm long, entire to weakly crenate at margins, rounded to subcuneate at base, glabrous on both surfaces, terminal lamina 12–30 × 6–18 cm, lateral laminas equal or slightly smaller than the terminal one; primary veins 8–13 pairs, plane above, prominent beneath; venation prominulous beneath. Peduncles 6–10 cm long, glabrous, sparsely lenticellate towards base. Inflorescences clustered racemes; rachis 1–4.5 cm long, glabrous; flowering pedicels 4–6 cm long, 5–8 cm thick, glabrous, ebracteolate. Calyx campanulate, ca 2 cm long, glabrous on exterior; lobes 5, rounded. Corolla ca 6–7 cm long, elliptic, glabrous, deep red on exterior, paler within. Stamens extremely numerous, over 700, the filaments caducous as a unit, united at base up to 2 mm, and then dividing into fused groups before becoming free above, the outer ones 7–8.5 cm long including base, yellow, apical portion tuberculate, with many shorter inner filaments from 3.5 cm long and of all intermediate sizes, the inner filaments tuberculate at apex only; anthers small. Ovary globose, 4-locular, glabrous on exterior. Styles 4, filamentous, 8–9 cm long, glabrous. Fruit subglobose to sublobate, to 15 cm long; exocarp glabrous, lenticellate; pericarp very thick and fleshy, detaching from mesocarp and endocarp; the mesocarp and endocarp enveloping seed to form a large stone ca 7 cm broad, 5 cm long, the mesocarp becoming lignified and hard, the exterior undulate, with short rounded tubercules; endocarp with tuberculate exterior and hard thin woody interior ca 1 mm thick; with 1–2(–4) subreniform seeds developing, 2 × 3 cm.

Additional material examined: PANAMA. DARIÉN: summit of Cerro Pirre, 29.XII.1972, *Gentry & Clewell 7023* (MO, NY). GUYANA. NW Dist., Hossororo, 12.VII.1934, fl., *Archer 2238* (K, US); Cuyuni-Mazaruni, Isseneru Creek, 6.45611, -60.341944, 2.XI.2006, fl., *Redden et al. 4923* (F, MO, US); Mazaruni Station, 10.XII.1937, fl., *Davis 546 (F.D.2576),* (K); Potaro-Siparuni Distr. Iwokrama, Siparuni R, Pakatau falls, 4.7917, -59.0106, 2.XII.1994, *Mutchnick & Allcock 490* (US). SURINAME. Nickerie, 1.III.1924, *B.W. 6440* (BM, MO, NY, U, WIS); Maratakka, 4.II.1915*, B.W. 918* (K, U); km 25 along railway, Saramacca, 7.I.1944, *Stahel 195* (L, U, USw, WAG). VENEZUELA. BOLÍVAR: Dist. Piar, SW slope Amaruay-tepui, E. of Auyan-tepui, 700-800 m, 26.IV.1986, fl., *Holst & Liesner 2726* (MO, NY).

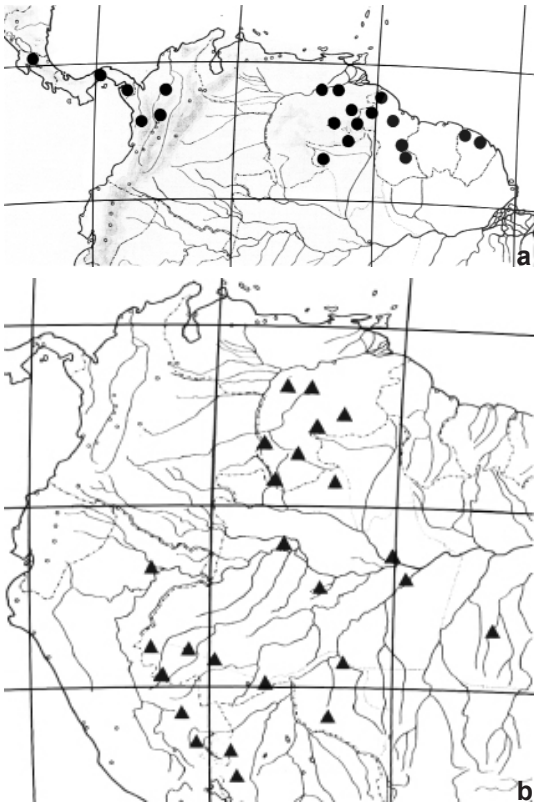

Figure 6 – a-b. Distribution of *Caryocar* species – a. *C. nuciferum*; b. *C. pallidum*; (based in Prance & Silva (1973)).

DELTA AMACURO: E of Rio Grande ENE of El Palmar, 25.II.1964, *Berti 101* (BR, COL, IPA, K, MO, NY, P, RFA, S, U, US, VEN). COLOMBIA. AMAZONAS: Río Caquetá, 2.5 km below Quebrada El Engaño, 1,100 m, 13.V.1988, *S. Sanchez 403* (K). BOLÍVAR: Serrania de San Lucas, Vereda La Libertad, 150 m, 19.VII.1887, *V. Cuadros 3560* (MO). BOYACÁ: region of Mt. Chapon, 6.VIII.1932, *Lawrence 394* (F). CHOCÓ: Río Negro between Quibdó and Tutenendo, 4.IV.1958, *Cuatrecasas & Llano 24217* (US); road between Yuto & Certegui, 100 m, 17.VIII.1976, fl., *Gentry & Fallen 17794* (COL, MO, NY). BRAZIL. RORAIMA: Base, Euclides da Cunha, IV.1948, fl., *Fróes 23167* (IAN). TRINIDAD, cultivated Port-of-Spain, Botanic Garden, 20.III.1945, fl. and fr., *Ewan 17000* (MO).

Known as the *souari nut* or *butter nut*, this tree is widely cultivated for the edible nut which used to be exported commercially from the Guianas and is used widely by the Indians and natives as a source of food. It is cultivated in the West Indies and grown in botanic gardens around the tropics. The seed is eaten raw or roasted and also yields an edible oil. The wood is used in boat making.

This species is easily distinguished from the other species of *Caryocar* since both the flowers and the fruit are very much larger. Linnaeus refers to Allamand twice in his description of *C. nuciferum*, and the material described by Linnaeus was undoubtedly an Allamand collection. Allamand material was deposited in the Linnaean herbarium, and since there is no specimen of *C. nuciferum* in that herbarium the whereabouts of the type is unknown and so I have designated a neotype from Suriname where Allamand collected. The neotype has both flowers and fruit and is well distributed to herbaria

Part of Aublet's species *Pekea tuberculosa* is synonymous with *C. nuciferum*. The fruit of *C. nuciferum* is quite distinct from any other fruit of this genus and is certainly that illustrated by Aublet for *Pekea tuberculosa*. There is no fruit with the Aublet herbarium material at the British Museum, and the leaves of *P. tuberculosa* are certainly not those of any species of Caryocaraceae. *Pekea tuberculosa* was described from a mixed collection. I have so far not been able to match the Aublet leaves but they are probably Bombacaceae or Sterculiaceae. Later authors increased the synonymy of this species by creating three other names for *Pekea tuberculosa* of Aublet, which are cited above in the synonymy of *C. nuciferum*.

The species is native of the primary forests of the Guianas and adjacent Venezuela and Brazil, but also cultivated outside this range. Forest on non-flooded ground.

Illustrations in Curtis's Botanical Magazine plates 2,727 (flower), 2,728 (fruit), (1827) in colour; Van Houtte, Flore des Serres 3: 182-184. 1847, colour; Wittmack, Martius *Flora brasiliensis* 12(1) t.69, I-IX (fruit); Prance (1998, fig. 121).

Local names: Venezuela: *almendra, imbe* (Arekuna), *impê-yek* (Arekuna); Guyana: *kola, sawarie, souari*; Suriname: *fireberoe, oera, kola, ingi notto, sawali, soeariew, sawari-noot*; English: *souari nut, butter nut*.

Caryocar nuciferum is listed as data deficient (DD) by IUCN, probably should be listed as vulnerable (VU).

1.15. *Caryocar pallidum* A.C. Smith, Jour. Arnold Arb. 20: 297. 1939.
Type: BRAZIL. AMAZONAS: Humaitá, between Rios Livramento and Ipixuna, 18.XI.1934, *Krukoff 7011* (holotype NY00429025; isotypes A00062685, BM000603042, BR0000006985622, F V0053251, K000432517, K000432516, LE, MO-279616,

RB00538055, RB00541116, S-R-11453, U0000978, US01013733, US1660987, USW8101). Fig. 6b

Tree to 40 m tall, young branches glabrescent. Leaves trifoliolate; petioles 2–12 cm long, terete, glabrous; leaflets shortly petiolulate, the terminal petiolule 7–10 mm long, the lateral petiolules shorter than the terminal one; the petioles glabrous, shallowly bicanaliculate; stipels 5–10 mm long, persistent, recurved, glabrous, membraneous; laminas elliptic, usually slightly asymetrical, acuminate at apex, acumen 5–12 mm long, cuneate or subcuneate and often unequal at base, conspicuously serrate at margins, glabrous on both surfaces, terminal lamina 8–17 × 3–8 cm, lateral laminas equal or slightly smaller than the terminal one; primary veins 11–13 pairs, plane above, prominent beneath; venation plane to prominulous beneath. Peduncles 7.5–13 cm long, glabrous, lenticellate, terete. Inflorescences clustered racemes, 17–25-flowered, the rachis 2.5–4 cm long, glabrous; flowering pedicels 1.6–3.5 cm long, glabrescent, ebracteolate. Calyx cupuliform, 7–11 mm long, glabrous on exterior; lobes 5, rounded, with ciliolate margins. Corolla 1.5–2.5 cm long; lobes 5, oblong, yellowish-white. Stamens numerous, ca 365; filaments shortly united at base into a single caducous unit, 2–3 cm long, yellowish-white, the apical portion tuberculate, the inner row of filaments with a few much shorter ones 1–1.5 cm long, tuberculate for entire length, the anthers small. Ovary globose, 4-locular, glabrous on exterior. Styles not seen. Fruit ellipsoid-globose, ca 5 × 5–7 cm, usually 1-locular, exocarp glabrous, crustaceous, remaining attached to mesocarp; mesocarp fleshy; endocarp of numerous fine spines 5–10 mm long and a hard, woody interior ca 2 mm thick.

Additional material examined: VENEZUELA. AMAZONAS: Río Cunucunuma, Monadnock, 20 mi above Playa Alta, 28.XII.1950, fl., *Maguire et al. 30439* (INPA, MO, NY, US); Dept. Atures, Río Ocamo, 31 km above confluence with Orinoco, 02°48'N, 65°05'W, 255 m, II.1990, *Fernández 7289* (K, PORT). BOLÍVAR: Río Uonán, trib Ikabarú, Caroní, X.1946, fl., *Cardona 1703* (NY, US, VEN). Raul Leoni, 64 km SE of Pijiguaos, 06°09'N, 66°23'W, 550 m, VII.1989, *Delgado 323* (K, PORT). BOLIVIA. LA PAZ: Mapiri region, San Carlos, XII.1926, fl., *Buchtein 1640* (US). Abel Iturralde Prov, Alto Madidi, opposite mouth Río Enlagua, 280 m, -13.58333, -68.76666, 23.V.1990, *Gentry & Estenssoro 70432* (K, LPB, MO). PERU. LORETO: Maynas, Puerto Almendras, 2.VIII.1973, *Ayala 322* (MO). MADRE DE DIOS: Manu, Cocha Cashu Biological Station, VIII-IX.1989, *Nuñez et al. 11390* (MO). PUNO: between Río Candamo & Río Guacamayo, 400-600 m, -13.50000, -69.833333, 22.V.1992, *Gentry et al. 76954* (MO). BRAZIL. ACRE: Serra do Moa, Mecânico Lima, 24.IV.1971, fr., *Prance et al. 12366* (INPA, NY, US). Plácido de Castro, km 20 AC-40, 10°15'45"S, 67°36'46"W, 5.II.2000, *Rivero et al. 369* (K, NY). AMAZONAS: Manaus, Reserva Florestal Adolfo Ducke, 15.XII.1995, fr., *Assunção 268* (INPA, K, MO, NY). RORAIMA: Vicinity of Auaris, 24.VII.1996, fr., *Prance et al. 21357* (INPA, K, NY, MO, US). RONDÔNIA: Porto Murtinho, Rio São Miguel, -12.0522, -63.5675, 17.XI.1996, fl., *Lobato et al. 1167* (HFSL).

The fruit of this species is an important food for the Yanomami at Homoxi.

This species is closely related to *C. glabrum*, but differs in the deeply serrate leaf margins, the thinner and less lenticellate rachis and pedicels and usually in the presence of large, recurved membraneous persistent stipels. A table showing the characteristics separating *Caryocar pallidum, C. glabrum* and *C. montanum* is given in Prance & Silva (1973).

The species is found in Venezuela and Amazonian Brazil and Bolivia. Forest on non-flooded ground.

Illustrations in Prance & Silva (1973); Prance (1998, fig. 120).

Local names: Brazil: *pequiarana*; Venezuela: *almendron; seso, xooxomohi* (Yanomami).

1.16. *Caryocar villosum* (Aublet) Persoon, Syn. 2: 84.1806.

Souari villosa Aublet, Pl. Guiane 1: 601, *t. 241*. 1775.

Pekea butyrosa Aublet Pl. Guiane 1: 594, *t. 238*. 1775, pro parte quoad fructus et flores tantum. Type: FRENCH GUIANA, *Aublet*, fruit only (BM).

Rhizobolus butyrosus (Aublet) Gmelin, Linn. Syst. Nat. ed. 13. 2(1): 840. 1789, pro parte.

Pekea villosa (Aublet) Poiret, Encyc. Méth, 5: 148. 1804.

Caryocar butyrosum (Aublet) Willdenow, Linn, Sp. Pl. ed. 4. 2:1243. 1799, pro parte.

Caryocar villosum var. *macrophyllum* Wittmack, Mart. *Fl. bras.* 12(1): 354. 1886. Type: BRAZIL. PARÁ: Belém, *Burchell 9861* (K000432514).

Caryocar villosum var. *aesculifolium* Wittmack, Mart. *Fl. bras.* 12(1): 354. 1886. Type: BRAZIL. PARÁ: *Martius* (holotype M0213167; isotypes M0213168. M0215169).

Type: FRENCH GUIANA. *Aublet* (BM; photo NY). Fig. 7

Tree to 40 m tall and up to 2.5 m diameter, young branches villous-tomentose, becoming glabrous with age. Leaves trifoliolate; petioles 4–15 cm long, villous-tomentose to puberulous, terete to slightly striate; leaflets shortly petiolulate, terminal petiolule 3–6 mm long, lateral petiolules

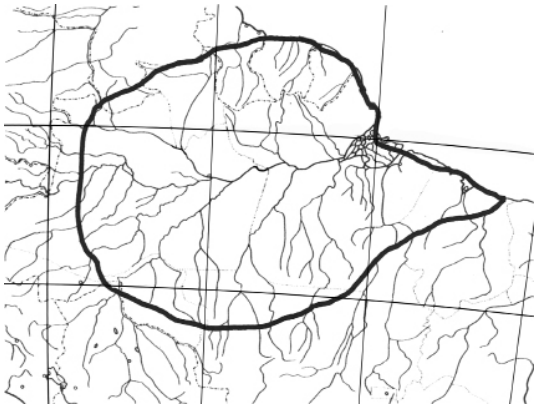

Figure 7 – Distribution of *Caryocar* species – *C. villosum*. (based in Prance & Silva (1973)).

2–4 mm long; petiolules puberulous when young, canaliculate; stipels absent; laminas elliptic, acuminate at apex, acumen 3–10 mm long, serrate to crenate at margins, rounded to cordate at base, villous to glabrous above, densely villous-hirsute or with a sparse pubescence on the venation only beneath, the terminal lamina 8–22 × 6–12 cm, lateral laminas slightly smaller; primary veins 12–19 pairs, slightly impressed or plane above, prominent beneath; venation extremely prominent beneath. Peduncles 5–13 cm long, tomentellous or puberulous when young, glabrescent, lenticellate. Inflorescences clustered racemes; rachis 3–4 cm long, tomentose when young; flowering pedicels 1.8–3.5 cm long, puberulous to glabrous, with 2 membraneous subpersistent bracteoles. Calyx campanulate-cupuliform, ca 1.5 cm long, gray puberulous to glabrous on exterior; lobes 5, rounded. Corolla ca 2.5 cm long; lobes 5, oblong-elliptic, pale yellow. Stamens numerous, ca 300, the filaments shortly united into a ring at base but not into groups, subpersistent, of two distinct lengths with several of intermediate lengths, the longest ca 6.5–7 cm long, yellow, the apical 1–3 mm tuberculate, the shortest ca 55, 1–1.5 cm long, with distinct fused portion at base, tuberculate entire length, the anthers small. Ovary globose, 4-locular, glabrous on exterior. Styles 4, filamentous, equalling filaments, glabrous. Fruit oblong-globose, 6–7 cm long, 7–8 cm broad; exocarp glabrous, lenticellate; pericarp thick, fleshy, detaching from mesocarp and endocarp; mesocarp and endocarp enveloping seed to form a reniform stone ca 5 cm broad, the exterior of mesocarp smooth and undulate the interior enveloping endocarp spines; endocarp with numerous fine spines ca 3 mm long and a hard woody interior ca 1 mm thick. 2n = 46.

Additional material examined: VENEZUELA: AMAZONAS, Río Maruca, Alto Orinoco, 1972, fl., *Lizot 4* (NY, VEN85802). FRENCH GUIANA. St. Laurent, XII.1956, fr., *Serv. For. BAFOG 20N* (U). BRAZIL. ACRE: track Boca do Acre to Monteverde, N bank Rio Purus, 21.IX.1966, fl., *Prance et al. 2490* (INPA, K, NY). AMAZONAS: Manaus, X.1851, fl., *Spruce 1819* (BM, CGE, G, GH, GOET, F, K, LD, LE, M, MG, NY, OXF, P); Reserva Ducke, 02º53'S, 59º58'W, 5.VII.1994, fl., *Nascimento 523* (INPA, K). AMAPÁ: Rio Iaue, 2 km from confl with Rio Oyapoque, 2.88, -52.37, 27.VIII.1960, fl., *Irwin et al. 47889* (G, GH, NY, UC, US, VEN). PARÁ: Belém, south woods of IAN, 26.I.1943, fl., *Archer 8202* (F, IAN, K, NY, UC, US); km 1180 Cuiabá-Santarém, 17.XI.1977, fr., *A. Silva 214* (IAN, K, MG, MO, NY). RONDÔNIA: km 117 Porto Velho to Cuiabá, 15.VIII.1968, fl., *Prance & Ramos 6992* (INPA, K, NY, US). RORAIMA: Serrinha, Rio Mucajaí, 31.I.1967, fl., *Prance et al. 4200* (F, INPA, K, MG, NY, US). BRAZIL. Maranhão: Rio Maracassumé, Estrada da Feitoria, São Bernardo, 20.X.1932, fl., *Fróes 1951* (A, BM, G, K, MO, NY, P, S, U). BRAZIL. MATO GROSSO: 16 km W of Alta Floresta on MT220, -9.9, -56.25, 1.X.1985, fl., *Thomas et al. 4135* (MO, NY, SPF, US).

The fruit has an edible pulp and edible cotyledons. The pulp is eaten most often and has a faint smell of rancid butter. It is also used to produce an edible oil. The wood has a fine straight grain and is used in heavy construction and in boat building. The pericarp is rich in tannins and has been used as a yellow dye by some indigenous groups.

This species is pollinated by bats (*Phyllostomus discolor*) and glossophaginae, but the flowers are also visited by arboreal marsupials and Sphingidae moths according to Martins & Gribel (2007).

Part of Aublet's species *Pekea butyrosa* also belongs to *Caryocar villosum*. The 5-foliate leaves of *P. butyrosa* are not those of Caryocaraceae, and consequently the identity of *P. butyrosa* has long remained uncertain. However, an Aublet fruit collection labelled *P. butyrosa* deposited in the carpological collection at BM matches well the distinctive fruit of *C. villosum* with the persistent mesocarp enveloping the endocarp spines. The fruit illustrated by Aublet is almost identical to the one at BM. The flowers of *P. butyrosa* which are not accurately drawn by Aublet, are also those of *C. villosum*. Thus, both species of *Pekea* were based on mixed collections, and the leaves and fruit of *C. villosum* were described in two different genera by Aublet. *Souari villosa* of Aublet represented

the leaves of the species now called *Caryocar villosum*, while *Pekea butyrosa* represented the flowers and fruit of the same species mixed with the wrong leaves. Fortunately no name changes are necessary since *S. villosa*, for which a good type specimen exists, can be taken as the basionym for this species, rather than *P. butyrosa*, a species based on mixed materials.

The species is found in French Guiana and Amazonian Brazil, most abundant in eastern Amazonia.

Illustration in Prance & Silva (1973).

Local names: Brazil: *Pequiá, Ruamahi* (Yanomami), *pekeá, petiá, piqui, piquiá, piquiá verdadeiro, piquiá-verdadeiro, suar*i; Guyana: bats suari; Venezuela *Kumato* (Yanomami).

Caryocar villosum is listed as Least concern (LC).

Excluded species

1.17. *Caryocar punctatum* Miquel *ex* Wittmack, Mart. *Fl. bras.* 12(1): 355. 1886, nom. nud. Type: SURINAME, *Hostmann & Kappler 1641* (G, LE, MO, S, U) = *Eriotheca globosa* (Aubl.) Robyns (Bombacaceae).

2. Anthodiscus.

Anthodiscus G.F.W. Meyer, Prim. Fl. Esseq. 193-195. 1818. Type: *Anthodiscus trifoliatus* G.F.W. Meyer.

Trees or shrubs. Stipules absent. Leaves alternate, long petiolate, trifoliolate; leaflets with short petioles, pinnately nerved, the margins usually crenulate or entire. Stipels absent. Inflorescences of terminal elongate botryoids; pedicels articulate. Bracteoles alternate, small, persistent or caducous. Flowers hermaphrodite, medium sized. Calyx cupuliform with very small reduced indistinct dentate lobes. Petals 5, imbricate, circumscissile at base and fused at apex to form a caducous calyptra. Stamens 100–280, filaments of varied length, the outermost always longer than the innermost, the interior filaments erect and smaller in bud, outer filaments recurved towards apex in bud, apical portion of all filaments tuberculate; anthers bilocular, small, introrse. Ovary 8–12(–15)-locular with a single ovule in each loculus, unitegmic. Styles 8–15 filiform, compound, equalling the number of locules of the ovary. Fruit 8–15 locular drupe with most loculi developing; pericarp thick, woody, hard, ridged on exterior but smooth not muricate. Seeds small, laterally compressed, the embryo with a spirally twisted radicle.

The name *Anthodiscus* is derived from the Greek words *ανςοσ* - andos = flowers and *ςΙθοσ* - diskos = disc, referring to the circular disc-shaped calyx.

Distributed mainly in the Guianas, Venezuela and western Amazonia, extending westwards to the Andes in Colombia and Peru, and in Chocó, Colombia and with one species as far north as Costa Rica and one disjunct to the Brazilian Atlantic rainforest.

A map of the distribution of all species of *Anthodiscus* was given in Prance & Mori (1980), but the distributions of several species has increased considerably since the monograph of Prance & Silva (1973), particularly the discovery of *Anthodiscus amazonicus* in the Atlantic coastal forest of Bahia, and of description of *A. chocoensis* west of the Andes and extending into Central America.

Key to species of *Anthodiscus*

1. Leaflets acuminate; the acumen 5–20 mm long.
   2. Petioles 4–6 cm long; leaflets membraneous; the acumen 10–20 mm long .... 2.3. *Anthodiscus klugii*
   2’. Petioles 1.5–3 cm long; leaflets coriaceous; the acumen 4–15 mm long.
      3. Terminal petiolule 15–20 mm; apical leaflet 6–7 cm broad; midrib slightly impressed above; peduncles c. 7 cm ..... 2.2. *Anthodiscus chocoensis*
      3’. Terminal petiolule 2–6 mm; apical leaflet 3.5–5 cm broad; midrib prominulous; peduncles 1.5–2.5 cm ..... 2.9. *Anthodiscus trifoliatus*

1’. Leaflets shortly cuspidate, rounded or emarginate.
   4. Leaflets and veins pilose on undersurface; petioles pilose tomentellous, 4–5 mm long; Peru, Loreto ..... 2.8. *Anthodiscus pilosus*
   4’. Leaflets and veins glabrous on undersurface; petioles glabrescent, 1–3 cm long.
      5. Botryoids short and clustered, 1–4 cm long; Colombia ..... 2.5. *Anthodiscus montanus*

5’. Botryoids elongate, 6.5–15 cm long.
  6. Leaf margins almost entire to obscurely crenulate, revolute.
    7. Leaflets broadly obovate; inflorescences with persistent lanceolate bracteoles; Upper Rio Negro.....2.6. *Anthodiscus obovata*
    7’. Leaflets oblong to ovate-elliptic; bracteoles caducous; Venezuela, Guyana.....2.4. *Anthodiscus mazarunensis*
  6’. Leaf margins conspicuously crenate.
    8. Axils of primary leaflet veins pubescent-barbate; Peru .....2.7. *Anthodiscus peruanus*
    8’. Axils of primary leaflet veins not barbate; Amazonia.....2.1. *Anthodiscus amazonicus*

2.1. *Anthodiscus amazonicus* Gleason & A.C. Smith, Brittonia 2: 156. 1936.
Type: BRAZIL. AMAZONAS: Humaitá, Livramento, 12.X.1934, fr., *Krukoff 7017* (holotype NY00429001; isotypes A00062673, BM000603052, BR0000005059881, F V0053230, G00226252, IAN044156, INPA16073, K00432573, LE, MICH1192000, MO1913799, NY00429001, RB00538048, S-R-11457, U0000969, US00113829; US01013731, US01013732 frag, INPA). Fig. 8a

Tree to 40 m tall, young branches puberulous-glabrescent. Leaves with stipules caducous, trifoliolate; petioles 1.5–3 cm long, terete, sparsely puberulous; leaflets petiolulate, the terminal petiolules 4–8 mm long, lateral petiolules shorter than the terminal one, petiolules sparsely puberulous, canaliculate; laminas oblong, thinly coriaceous, more or less symetrical, retuse at apex, cuneate at base, crenate at margins, the teeth narrow, glabrous above, glabrous beneath except for slightly puberulous midrib, terminal lamina 6–8.5 × 2.2–3.5 cm, lateral laminas smaller than the terminal one; midrib plane to slightly impressed and glabrous above, prominent and sparsely puberulous to glabrous beneath; primary veins 8–11 pairs, prominulous on both surfaces. Peduncles 2–5 cm long, sparsely puberulous, terete, not conspicuously lenticellate. Inflorescences elongate botryoids, 30–40-flowered; rachis 8–13 cm long, sparsely puberulous, flowering pedicels 4–9 mm long, puberulous or sparsely puberulous, ebracteolate. Bracteoles caducous. Calyx broadly cupuliform, 2–3 mm long, puberulous on exterior, 5-pointed. Corolla 6–8 mm long; lobes 5, but remaining attached at apex to form a calyptra, and circumscissile at base, yellow. Stamens numerous, ca 170; filaments free almost to base, 4–9 mm long, apical portion tuberculate; anthers small. Ovary globose, glabrous on exterior, 12-locular. Styles 11–14, ca 3 mm long, glabrous. Fruit flattened, globose, ca 2.2 cm broad, 1 cm long, slightly ribbed at maturity, 12-locular; exocarp smooth, glabrous; pericarp thick, hard, glabrous within.

Additional material examined: COLOMBIA. Amazonas: Río Caquetá, Caño Solarte, 200 m, 21.VIII.1986, fl., *Palacios et al. 1823* (K). VAUPÉS: Río Apaporis, entre ríos Kananarí y Pacoa, 1.XII.1951, fl., *García-Barriga 13980* (COL); Confluence Rios Guainía & Negro, 13-17.XII.1947, fl., *Schultes & López 9387* (COL, F, IAN, K, NY, U, US). ECUADOR. MORONA-SANTIAGO: road Mendez-Morona, 650 m, -3.000, -78.166666, 17.VIII.1989, fl., *Van der Werff & Gudiño 11174* (MO); Parroquia Bomboiza, Misión Salesiano Shuar Húmedo premontano, 800 m, -3.41666, -78.58333, 3.XI.1986, fl., *Cerón et al. 435* (MO, NY, QAME). NAPO: Est. Biol. Jatun Sacha, Río Napo, 8 km E of Misahualli, -1.06666, -77.60000, 10.VIII.1989, fl., *Cerón 7364* (ECUAMZ, K, LOJA, MO, QCNE). ORELLANA: Parque Nacional Yasuní, Carretera Popeya Sur-Iro, -0.64250, -76.46444, 27.V.1997, *Macía et al. 564* (MO, QCA). PERU. AMAZONAS: road Chiriaco-Bagua, -5.28250, -78.38611, 20.III.2001, fr., *der Werff et al. 16270* (MO). LORETO: Maynas, Yanayacu, 110 m, -3.75000, -72.91666, 6.X.1988, fl., *Vásquez et al. 11150* (MO). MADRE DE DIOS: Tambopata, 26 km S of Puerto Maldonaldo, 280 m, -12.81666, -69.28333, 12.XI.1989, fl., *Hartshorn 2422* (MO). PASCO: Oxapampa, Distr. Palcazú, -10.225277, -75.2241, 26.IX.2010, fr., *Vásquez et al. 36815* (HOXA, HUT, MO, USM). PUNO: Carabaya, Río Candamo, 400 m, -13.41666, -69.91666, 9.III.1997, fr., *Cornejo & Balarezo 2917* (MO). UCAYALI: Distr. Raimondi, Comunidad Nativa Aerija, 625 m, -10.74000, -73.813333, 13.VII.2015, fl., *OSINFOR JRA3* (MO). VENEZUELA. AMAZONAS: Dpt. Casiquiari, Río Casiquiare, El Porvenir, 02º02’N, 66º29’W, 13.II.1991, fr., *Colella & Guayamere 2126* (K, NY). BRAZIL. ACRE: Cruzeiro do Sul, BR-307, near intersection with Ramal Pentecostes, 07°24’4.2”-26.8’58”S, 73°01’17.16”-72°58’9.18”W, 12.XII.2000, fl., *Daly et al. 10652* (K, NY). AMAZONAS: Foz de Jutaí, 19.XI.1927, fl., *Ducke RB21094* (G, K, RB, S,

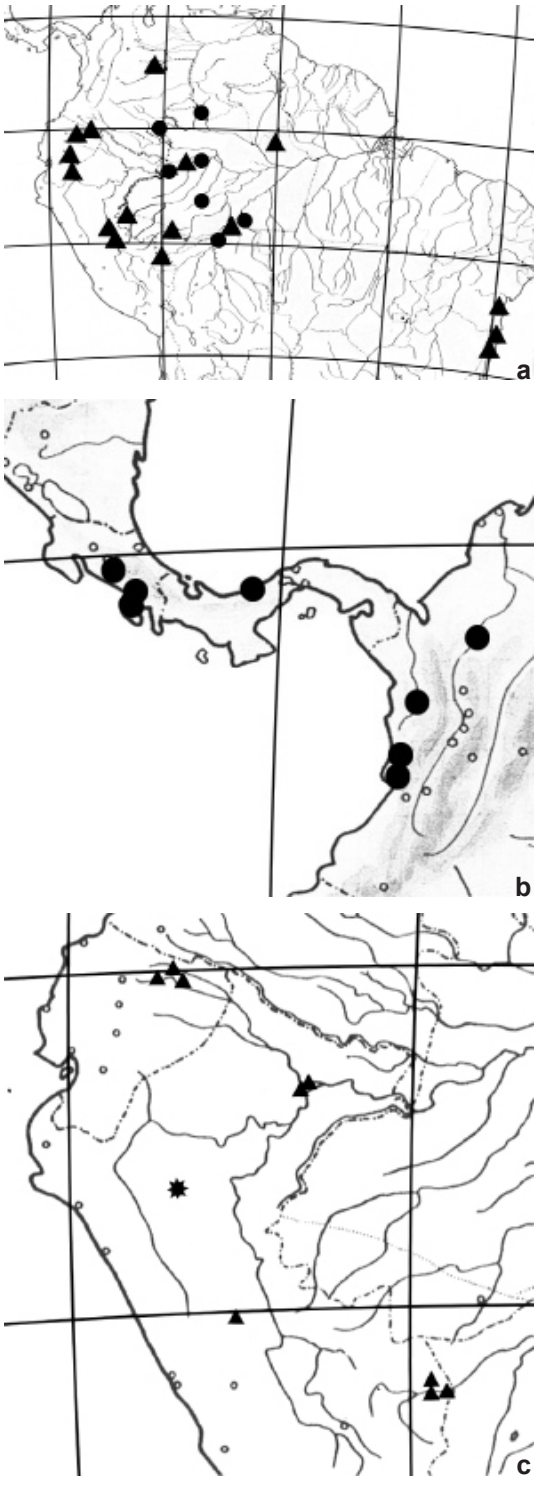

Figure 8 – a-c. Distribution of *Anthodiscus* species – a. *A. amazonicus*, circles = known distribution in 1973; b. *A. chocoensis*; c. *A. klugii*, star = known distribution in 1973. (based in Prance & Silva (1973)).

U). RONDÔNIA: Mutumparaná airstrip, 25.XI.1968, fl., *Prance et al. 8849* (F, INPA, K, MG, MO, NY, US). BRAZIL. BAHIA: Santa Cruz de Cabrália, 15 km NW of Porto Seguro, *Mori et al. 11863* (CEPEC, NY). Una, km 46 BA-001 Ilhéus-Una, Reserva Micoleão, -15.15000, -39.083333, 1.VI.2000, fr., *Sant'Ana et al. 878* (CEPEC, MO, NY).

The fruit is used as a humming top by the Deni Indians. They insert a central spindle, hollow out the centre and make 2 holes in the side. This is spun at high speed with use of a string and is a plaything of both children and adult members of the tribe.

Prance & Mori (1980) reported the relatively recent discovery of the unusual disjunct distribution of this species into the Atlantic Coastal forests of Brazil.

The species is distributed in Western Amazonia and disjunct to the Atlantic rainforest of Bahia, Brazil. High forests on non-flooded ground.

Illustrations in Perdiz *et al.* (2012: 111); map, Prance & Mori (1980).

Local names: *tetiarú* (Deni); Brazil: *pequi-mirindiba*.

Anthodiscus amazonicus is listed as Least Concern (LC) by IUCN.

2.2. *Anthodiscus chocoensis* Prance, Brittonia 32: 530. 1980.

Type: COLOMBIA. CHOCÓ: 30 km S of Quibdó road to Lloró, 1-2 km S of Yuto, 7.I.1979, fl., *A. Gentry & E. Renteria A. 23801* (holotype COL000002638; isotypes HUA0000179, MO-197446, NY). Fig. 8b

Tree 40 m tall, young branches glabrous. Leaves without stipules; petioles 1.5–2.2 cm long, terete, sparsely puberulous; leaflets petiolulate, terminal petiolule 1.5–2 cm long, lateral petiolules shorter than terminal one, petiolules sparsely puberulous, canaliculate above; laminas elliptic, coriaceous, symmetrical or slightly asymmetrical, acuminate at apex, acumen 5–15 mm long, cuneate at base, margins crenate, glabrous on both surfaces except for a few appressed hairs on the lower surface of midrib, terminal lamina 12–15 × 6–7 cm, lateral laminas smaller than the terminal one; midrib slightly impressed above, prominent beneath; primary veins 11–14 pairs, prominulous on both surfaces. Peduncles ca 7 cm long, sparsely puberulous, terete, not conspicuously lenticellate. Inflorescences elongate botryoids; rachis 5–6 cm long, sparsely puberulous; pedicels 5–6 mm long, sparsely puberulous, ebracteolate. Calyx

broadly cupuliform, ca. 2.5 mm long, 6 mm broad, puberulous on exterior, 5-pointed. Corolla yellow, remaining attached at apex of lobes to form a calyptra and circumscissile at base. Stamens numerous, ca, 150; filaments free almost to base, 3–5 mm long, apical portion tuberculate; anthers small. Ovary globose, glabrous on exterior, 12-locular. Styles ca. 32, 1.5 mm long. Fruit a flattened circular drupe, 1.8–2 cm broad, 1 cm long, slightly ribbed on upper part which is brown in fresh fruit, the lower part smooth and green, the whole markedly divided into two zones in fresh fruit; exocarp smooth, glabrous; pericarp thick, hard; dividing into 12 capsules each with a single seed, the seeds remaining in the capsules during germination.

Additional material examined: COSTA RICA. PUNTARENAS: Golfito, PN Corcovado, Osa Peninsula, 200-300 m, 8.2525, -83.42777, 8.V.1994, fr., *Aguilar 3256* (F, INB, K, MO). SAN JOSÉ: Pérez Zeledón, Río Nuevo, 1,204 m, 09º27'40"N, 83º51'20"W, 7.II.2001, *Estrada 2706* (CR, K). PANAMA. COLÓN: Donoso, 291 m, 8.83166, -80.684722, 17.V.2012, fr., *Hammel 26219* (MO). COLOMBIA. VALLE DEL CAUCA: Bajo Calima, 15 km N of Buenaventura, 50 m, 04°1'31"N, 77°04'47"W, 18.II.1983, fl. and fr., *Gentry & Juncosa 40460* (COL, MO, NY, US); 10 km N. of Buenaventura, Concesión Carton de Colombia, 640 m, 4.XII.1981, fl. and fr., *Gentry 35277* (COL, MO); road to Juanchaco Palmeras, 100 m, 10.VII.1984, fl., *Gentry et al. 47853* (MO, NY).

When described this species was only known from Colombia. More recently it has been shown to be common in Osa, Costa Rica and Panama.

Lowland forest to 200 m.

Illustration in Prance (1980).

Local name: Costa Rica: *ajo negro*.

Anthodiscus chocoensis is listed as Vulnerable (VU) by IUCN, threatened by habitat loss throughout its range.

2.3. *Anthodiscus klugii* Standley *ex* Prance, Brittonia 23: 443. 1971.

Type: PERU. SAN MARTÍN: Pongo de Cainarachi, Río Cainarachi, IX-X.1932, fl., *Klug 2682* (holotype NY429004; isotypes BM000603038, CAS0000471, FV0053233, G00226258, GH00062674, K000432567, MO-279620, S-R-11458, US00113831). Fig. 8c

Tree 6 m tall, young branches sparsely puberulous-glabrescent. Leaves with stipules lanceolate, ca 1.5 mm long, persistent, trifoliolate; petioles 2.5–6.5 cm long, terete, puberulous; leaflets shortly petiolulate, terminal petiolule 6–12 mm long, lateral petiolules much shorter than the terminal one, not exceeding 4 mm long, petiolules sparsely puberulous, shallowly canaliculate; laminas oblong-elliptic, symetrical, chartaceous, acuminate at apex, acumen 7–17 mm long, cuneate and almost equal at base, margins crenate, glabrous above except for sparsely puberulous-glabrescent lower portion of young midrib, glabrous beneath except for puberulous midrib and venation, terminal lamina 8.5–17.5 × 3.7–7 cm, lateral laminas conspicuously smaller than the terminal one; midrib slightly impressed to plane above; primary veins 9–10 pairs, plane above, prominent beneath, venation prominulous beneath. Peduncles 2–4.5 cm long, terete, sparsely puberulous. Inflorescences elongate botryoids, 20–30-flowered; rachis 5–6.5 cm long, sparsely puberulous; flowering pedicels 5–7 mm long, sparsely puberulous, ebracteolate. Calyx broadly cupuliform, 2–3 mm long, sparsely puberulous on exterior, 5 pointed. Corolla 5–6 mm long; lobes 5, but remaining attached at apex to form a calyptra, and circumscissile at base, yellow. Stamens numerous; filaments free almost to base, 5–8 mm long, yellow, apical portion tuberculate; anthers small. Ovary globose, 10–12-locular, glabrous on exterior. Styles 10–12, ca 1.5 mm long, glabrous. Fruit a flattened circular drupe ca 2 cm diam., exocarp smooth unridged, glabrous; pericarp thick, hard.

Additional material examined: BOLIVIA. LA PAZ: Alto Madidi, opposite mouth Río Enlatagua, -13.58333, -68.76666, 22.V.1990, *Gentry & Estenssoro 70350* (K, MO). ECUADOR. NAPO: Orellana, Yasuni National Park, kms 14-15 of Manus/YPF Pipeline road, 00°31'S, 76°32'W, 250 m, IX-X.1999, *Pitman & Delinks 2274* (K, MO, QCA, QCNE). PERU. PASCO: Oxapampa, Dist. Palcazu, Bosque de Protección San Matias-San Carlos, 374 m, -9.94194, -75.22805, 23.V.2008, fr., *Vásquez et al. 34234* (HOXA, HUT, MO, MOL, USM). SAN MARTÍN: Lamas, Convento, trail to Nuevo Lamas, -6.26666, -76.28333, 10.VIII.1986, fr., *Knapp & Mallet 6897* (MO, US).

This species is quite distinct from most species of the genus by the long thin acumen of the leaves, the larger membraneous leaves, and the distinct terminal petiolule.

The species is little-collected from San Martín, Peru and Napo, Ecuador south to Bolivia, lowland forest.

Illustration in Prance (1971).

Anthodiscus klugii is listed as Endangered (E) in Walter & Gillett (1998).

2.4. ***Anthodiscus mazarunensis*** Gilly, Trop. Woods 72: 16. 1942.

Type: GUYANA. Upper Mazaruni drainage near Haiamatipu mount, Arubaru River, 3.II.1939, *Pinkus 280* (holotype NY00429005; isotypes BR0000006986308, IAN095980, M0213166, NA0109929, RB00538049, S-R-11459, U0000970, US00113832, VEN), isotypes which differ in leaf shape and margins at: F0053234, G00226253, GH00062675, MO-279657. Fig. 9a

Tree to 25 m tall, young branches puberulous-glabrescent. Leaves with stipules lanceolate, to 6 mm long, membraneous, caducous, trifoliolate; petioles 0.8–4.5 cm long, puberulous to glabrous, terete; leaflets petiolulate, terminal petiolule 6–25 mm long, lateral petiolules shorter than the terminal one, petiolules puberulous, canaliculate; laminas obovate to oblong, slightly asymetrical, coriaceous, shortly mucronate, rounded or retuse at apex, cuneate and slightly unequal at base, slightly crenulate and revolute at margins, glabrous on both surfaces except for midrib beneath, terminal lamina 6–11 × 3–6.2 cm, lateral laminas smaller than the terminal one; midrib impressed and glabrous above, prominent and puberulous beneath; primary veins 8–12 pairs, prominulous on both surfaces. Peduncles 1–4 cm long, terete, sparsely puberulous, not conspicuously lenticellate. Inflorescences elongate botryoids, 20–40-flowered; rachis 4–9 cm long, sparsely puberulous; flowering pedicels 5–8 mm long, sparsely puberulous, ebracteolate. Bracteoles caducous. Calyx broadly cupuliform, 2–3 mm long, puberulous on exterior, 5 pointed. Corolla ca 7 mm long; lobes 5, remaining attached at apex to form a calyptra, and circumscissile at base, yellow. Stamens numerous, ca 115, the filaments free almost to base, 6–9 mm long, apical portion tuberculate; anthers small. Ovary globose, glabrous on exterior, 10–12-locular. Styles 10–12, 2–3 mm long, glabrous. Fruit flattened-globose, ca 10 mm broad, 7 mm long, slightly ribbed longitudinally when mature, but not pointed, 10–12-locular; exocarp glabrous, slightly ridged towards base; pericarp hard, rather thin, the interior glabrous.

Additional material examined: GUYANA. Kaietur Plateau, 11.V.1944, fl., *Maguire & Fanshawe 23398* (F, K, M, NY, S, U, UC, US); Cuyuni-Mazaruni, below Kamakusa Mt, Powis Creek, 5.80750, -60.23527, 662 m, 20.V.2012, fl., *Redden et al. 7265* (K, MO). SURINAME. Tafelberg, S rim Arrowhead Basin, 29.VIII.1944, fl., *Maguire 24576* (A, F, G, K, MO, NY, S, U, UC, US, VEN); Sipaliwini, Tafelberg Nat. Park, between N Ridge and Lisa's Creek, 3.91666, -56.18333, 28.VI.1998, fl. and fr., *Lohmann 190* (K, MO). VENEZUELA. AMAZONAS: Río Yatua, Cerro de Neblina, 16.I.1954, fl., *Maguire et al. 37340* (INPA, NY); Río Negro, Cerro Neblina base camp, 15 km NNE of Pico Phelps, 780 m, 0.85000, -65.95000, 14-18.III.1984, fl. and fr., *Liesner 16719* (K, MO). BOLÍVAR: Chimantá Massif, Río Tirica above Techiné-Merú, 470 m, 16.I.1995, fl., *Steyermark & Wurdack 115* (COL, F, GH, K, MO, NY, P, S, U, VEN). BRAZIL. AMAZONAS: Tunuí, Rio Içana, 1948, fl., *Black 48-2594* (IAN, US).

Anthodiscus mazarunensis is closely related to *A. obovatus*, and these two species may ultimately prove to be one rather variable species. The most obvious difference is the broadly orbicular leaves of *A. obovatus* compared with the narrowly obovate to oblong-elliptic leaves of *A. mazarunensis*. In *A. obovatus* the length/breadth ratio of the terminal leaflet is 1.23–1.72, while it is 1.75–2.24 in *A. mazarunensis*. In addition, *A. mazarunensis* differs from *A. obovatus* in the less pubescent pedicels and exterior of the calyx, in the absence of persistent bracteoles at the base of the pedicels, and in the tendency to slightly crenulate leaf margins.

The species is confined to the sandstone areas of Venezuela, the Guianas and adjacent Brazil. Sandy forest beside rivers.

Illustrations in Prance & Silva (1973); Prance (1998, fig. 116).

Local names: Venezuela: *epunodék* (Arekuna), *otoye-muyek* (Arekuna).

2.5. ***Anthodiscus montanus*** Gleason, Phytologia 1: 29. 1933.

Type: COLOMBIA. BOYACÁ: Mt. Chapon, El Humbo region, 130 mi NW of Bogotá, 1,000 m, 25.IX.1932, fl., *Lawrance 474* (holotype NY429006; isotypes BM000603041, CAS0000472, E00326633, F V0053235, G00226254, G00226255, GH00062676, INPA215496, K000432568, MO-279656, S-R-11460, U0000971, UC1293455, US00113833). Fig. 9b

Tree to 30 m tall, the young branches sparsely puberulous, soon glabrescent. Leaves with stipules lanceolate, ca 1.5 mm long, persistent, trifoliolate; petioles 1–2 cm long, terete, glabrescent; leaflets shortly petiolulate, terminal petiolule ca 1 mm long, lateral petiolules ca 0.5 mm long or leaflets sessile, petiolules sparsely puberulous, canaliculate; laminas obovate, symetrical, coriaceous, rounded to slightly acute at apex, cuneate at base, crenulate at margins, glabrous on both surfaces except for slightly

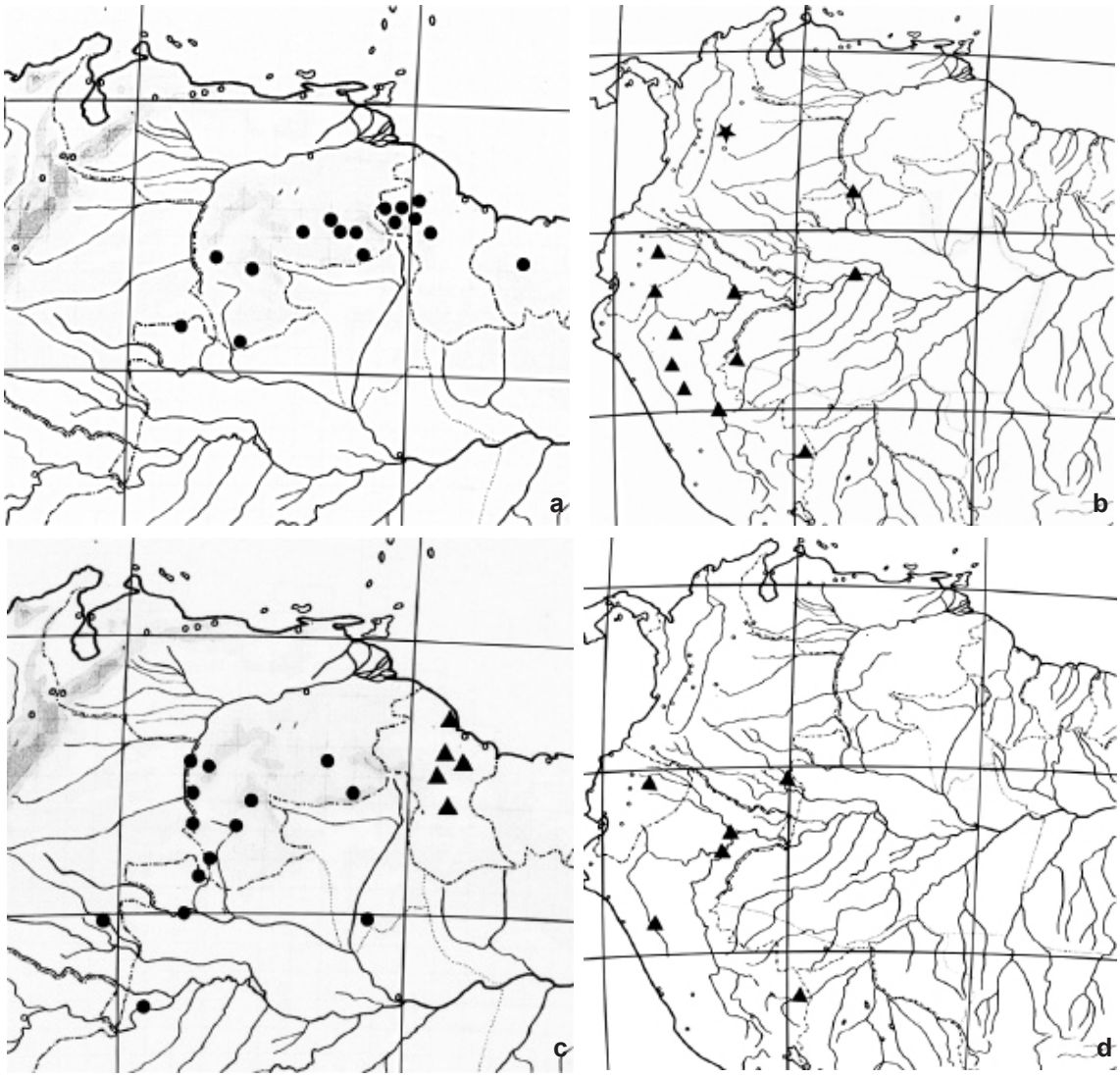

Figure 9 – a-d. Distribution of *Anthodiscus* species – a. *A. mazarunensis*; b. triangles = *A. peruanus*, star = *A. montanus*; c. circles = *A. obovatus*, triangles = *A. trifoliatus*; d. *A. pilosus.* (based in Prance & Silva (1973)).

puberulous midrib beneath, terminal lamina 4.5–7 cm long, lateral laminas equal or only slightly smaller than the terminal one; midrib plane to slightly impressed above; primary veins 5–8 pairs, prominulous above, prominent beneath. Peduncles 2–4.5 cm long, terete, puberulous, not conspicuously lenticellate. Inflorescences densely clustered botryoids, ca 25-flowered; rachis 1.5–2.5 cm long, puberulous; flowering pedicels 5–8 mm long, ebracteolate, puberulous. Calyx broadly cupuliform, ca 1.5 mm long, puberulous on exterior, 5 pointed, margins ciliolate. Corolla ca 5 mm long; lobes 5, but remaining attached at apex to form a calyptra, and circumscissile at base, yellow. Stamens numerous; filaments free almost to base, 3–7 mm long, yellow, the apical portion tuberculate, the anthers small. Ovary globose, 12-locular, glabrous on exterior. Styles 12, 1.5–2.5 mm long, glabrous. Fruit flattened-globose, ca 1.5 cm broad, 1 cm long, not conspicuously ribbed or pointed, 12-locular; exocarp glabrous, smooth; pericarp thick, hard smooth, the interior glabrous. **Additional material examined**: COLOMBIA. BOYACÁ: El Humbo, 130 mi N of Bogotá, 1,300 m, 16.V.1933, *Lawrance 802* (A, F, G, K, MO, S, UC, US).

The species is present in Colombia, known only from the forests north of Bogotá at 1,000–1,250 m altitude.

Anthodiscus montanus is listed as Endangered (E) in Walter & Gillett (1998) and listed as Endangered (EN) by IUCN. Calderon (1998). *Anthodiscus montanus*. The IUCN Red List of Threatened Species 1998.

2.6. *Anthodiscus obovatus* Bentham *ex* Wittmack, Mart. *Fl. bras.* 12(1): 358. 1886.
Type: VENEZUELA. AMAZONAS: San Carlos de Rio Negro, 1853-1854, *Spruce 3146* (holotype B, lost; photos, F, MO, NY; lectotype of Prance & Silva (1973) K000432670; isotypes BM000603045, BR0000005059898, C10009093, CGE, E00326632, F V0053236, G00226256, GH00062677, GOET000555, K000432569, LD2071290, LE, MPU014412, OXF, P01900561, P01900562). Fig. 9c

Tree to 8 m tall, the young branches puberulous-glabrescent. Leaves with stipules lanceolate, to 5 mm long, membraneous, caducous, trifoliolate; petioles 0.5–3 cm long, terete, glabrescent; leaflets petiolulate, terminal petiolule 8–15 mm long, lateral petiolules much shorter than the terminal one, petiolules glabrescent, canaliculate; laminas obovate-orbicular, slightly asymetrical, coriaceous, shortly mucronate at apex, mucro 0.5–3 mm long, cuneate at base, entire and slightly revolute at margins, glabrous on both surfaces, terminal lamina 8–11.5 × 5–8 cm, lateral laminas smaller than the terminal one; midrib impressed and glabrous above; primary veins 9–10 pairs, prominulous above, prominent and glabrous beneath. Peduncles 1.5–5.5 cm long, terete, puberulous-glabrescent, not conspicuously lenticellate. Inflorescences elongate botryoids, ca 40–50-flowered; rachis 6–13 cm long, puberulous; flowering pedicels 5–8 mm long, puberulous-tomentellous, ebracteolate. Bracteoles at base of pedicel, lanceolate, membraneous, persistent, ca 5 mm long. Calyx broadly cupuliform, ca 2.5 mm long, puberulous-tomentellous on exterior, 5 pointed. Corolla ca 6 mm long; lobes 5, often remaining attached at apex to form a calyptra, and circumscissile at base, yellow. Stamens numerous, ca 130; filaments free almost to base, 5–11 mm long, yellow, apical portion tuberculate; anthers small. Ovary globose, glabrous on exterior, ca 12-locular. Styles 11–12, ca 3 mm long, glabrous. Fruit flattened-globose, ca 10 mm broad, 7 mm long, slightly ribbed longitudinally but not pointed, 10–11-locular; exocarp glabrous, slightly ridged; pericarp thick, hard, interior glabrous.

Additional material examined: VENEZUELA. BOLÍVAR: *Cardona 1223* (US, VEN). AMAZONAS: Río Guainia, Pimichin-Yavita trail, 120-140 m, 10.X.1957, fr., *Maguire et al. 41796* (F, G, IAN, K, NY, S, U, VEN); Misión Río Mavaca, 01°58'N, 65°06'W, 3.II.1991, fr., *Stergios & Yánez 15111* (K). COLOMBIA. AMAZONAS-VAUPÉS: *García-Barriga 13736* (COL, NY, US). BRAZIL. AMAZONAS: Rio Curucuriarí, Cajú cataract, 18.XI.1936, fl., *Ducke 348* (A, F, K, MO, NY, US).

The bark used as an ingredient of the *Strychnos* based arrow poison of the Tukanos Indians and the plant as a fish poison (Kawanishi *et al.* 1986).

The species is distributed in Upper Rio Negro region of Colombia and Venezuela and extending to the state of Bolívar. Caatinga forests and riverbanks.

Illustration in Wittmack, Martius *Flora brasiliensis* 12 (1) t.74. 1886.

Local names: *tee-fĕ-roo'-ka* (Tanimuka); *ko-men'-tan-go, gaw'-we* (Makuna); *chee-aw'* (Makú).

Anthodiscus obovatus is listed as least concern (LC).

2.7. *Anthodiscus peruanus* Baillon, Adansonia 10: 241. 1872.
Anthodiscus glaucescens Macbride, Candollea 5: 385 (1934). Type: PERU. San Martín San Roque, 17.I.1930, *Ll. Williams 7491* (holotype F; isotype frag. G00226257).
Anthodiscus gutierrezii L.O. Williams, Fieldiana Bot. 31: 22 (1964). Type: PERU. HUÁNUCO: Leonico Prado, Hacienda Delicias, *Gutiérrez R. 14* (holotype F V0053232; isotypes, G, K000741714, NY00429002, S, US00113830, WIS00000715MAD, WIS0255874WIS).
Type: PERU. *Rivero C13* (holotype P01900560, photos F, MO; isotypes K000432571, MA813330, frag. F V0053237). Fig. 9b

Tree to 30 m tall, young branches puberulous-glabrescent. Leaves with stipules ca 2 mm long, caducous, trifoliolate; petioles 1.5–3 cm long, puberulous, terete; leaflets petiolulate, the terminal petiolule 4–7 mm long, lateral petiolules shorter than the terminal one, petiolules sparsely puberulous, canaliculate; laminas oblong, symetrical or only slightly asymetrical, chartaceous, acute, rounded or retuse at apex, cuneate at base, crenate at margins, the teeth wide, glabrous above, glabrous beneath except puberulous midrib and primary veins and their barbate axils, terminal lamina 6–9.5 × 2.5–4.8 cm, lateral laminas smaller than the terminal

one; midrib impressed and glabrous to sparsely puberulous above, prominent and puberulous beneath; primary veins 8–10 pairs, prominulous above, prominent beneath. Peduncles 3–5 cm long, terete, puberulous, not conspicuously lenticellate. Inflorescences elongate botryoids, 30–40-flowered, the rachis 6–8 cm long, sparsely puberulous; flowering pedicels 3–10 mm long, puberulous, ebracteolate. Bracteoles caducous (not seen). Calyx broadly cupuliform, 2–3.5 mm long, puberulous on exterior, 5 pointed. Corolla ca 7 mm long; lobes 5, remaining attached at apex to form a calyptra, and circumscissile at base, yellow. Stamens numerous, ca 150; filaments free almost to base, 4–8 mm long, apical portion tuberculate; anthers small. Ovary globose, glabrous on exterior, 12-locular. Styles 11–12, ca 1.5 mm long, glabrous. Fruit flattened-globose, ca 1.6 cm broad, 0.8 cm long, not ribbed or pointed, 12-locular; exocarp smooth, glabrous; pericarp hard, thick, glabrous within.

Additional material examined: ECUADOR. MORONA-SANTIAGO: Cordillera Cutucu, road Mendez-Morona, -2.916666, -78.166666, 800 m, 3.II.1989, fr., *van der Werff & Palacios 10348* (K, MO). NAPO: Jatun Sacha, 8 km below Misahualli, 450 m, -1.66666, -77.60000, 17.I-6.II.1987, fr., *Cerón, 885* (K, MO, QAME). PASTAZA: Pozo Villano 2 de Arco, 400 m, -1.41666, -77.33333., 3.XII.1991, fr., *Tipaz et al. 536* (K, MO). ZAMORA-CHINCHIPE: El Pangui, Cordillera de Cóndor, Río Wawaime, 1,200 m, -3.56694, -78.43166, 24.X.2006, fl., *van der Werff et al. 21671* (MO). PERU. AMAZONAS: Condorcanqui, Caterpiza, Río Santiago, 200 m, 17.IX.1979, fl., *Huashikat 633* (MO). HUÁNUCO: *R. Gutiérrez 68* (F, NY, S, US, WIS). LORETO: *Tessmann 4856* (G, NY). MADRE DE DIOS: Manu Prov. Puerto Maldonaldo, Los Amigos Biol. Station, -12.57, -70.1, 270 m, 9.VIII.2002, *Janovec & Maceda 2634* (BRIT, K). PASCO: Oxapampa, Reserva Comunal Yanesha, 500 m, -10.13444, -75.368333, 6.VIII.2008, fl., *Rojas & Ortiz 5970* (HOXA, MO, MOL, USM). SAN MARTÍN: Tocache Nuevo, towards Limón, 500 m, -8.166666, -76.53333, 11.III.1979, *Gentry et al. 25580* (MO). BRAZIL. ACRE: PN Serra da Divisor, Rio Azul, -7.70694, -73.28750, 11.V.1996, fr., *Daly 9027* (K, MO, NY).

The Kuripako Indians use this tree as a fish poison (Kawanishi *et al.* 1986).

This species is close to *A. amazonicus* and is most easily distinguished by the barbate mass of hair at the axils of the primary veins, it also differs from *A. amazonicus* in the tendency to larger leaves, the much coarser teeth of the crenate leaf margins, and the acute leaf apex in most specimens.

The species is distributed in forests of the eastern foothills of the Andes in northern Peru, Ecuador and adjacent Brazil.

lllustrations in Wittmack, Martius *Flora brasiliensis* 12(1) t. 74. 1886; Prance & Silva (1973).

Anthodiscus peruanus is listed as rare (R) in Walter & Gillett (1998).

2.8. *Anthodiscus pilosus* Ducke, Trop. Woods. 90: 23. 1947.

Type: PERU. LORETO: San Juan Nuevo, near Iquitos, 11.XII.1945, *Ducke 1855* (holotype RB; isotypes A00353507, F V0053238, GH00062678, IAN012455, K000432572, MG018644, NY429007, R000075501, R000075501a, U0000972, US03389329, frag. INPA15989). Fig. 9d

Tree to 25 m tall, the young branches tomentellous becoming glabrescent with age. Leaves with stipules oblong ca 1 mm long, persistent, trifoliolate; petioles 1–5 cm long, terete, tomentellous; leaflets shortly petiolulate, terminal petiolule 5–14 mm long, lateral petiolules shorter than the terminal one, petiolules pilose, canaliculate; laminas obovate, symmetrical, coriaceous, rounded to mucronate at apex, the mucro not exceeding 3 mm long, cuneate at base, crenate at margins, glabrous above except for sparsely puberulous midrib, sparsely tomentellous-pilose beneath especially on midrib and venation, terminal lamina 6–11 × 3–5 cm, lateral laminas smaller than the terminal one; midrib slightly impressed above; primary veins 10–12 pairs, prominulous above, prominent and tomentellous beneath. Peduncles 2–4.5 cm long, terete, tomentellous, not conspicuously lenticellate. Inflorescences elongate botryoids, ca 20–35-flowered; rachis 5–9 cm long, tomentellous; flowering pedicels 7–10 mm long, ebracteolate, tomentellous. Calyx broadly cupuliform, 1.5–2.5 mm long, tomentellous on exterior, 5 pointed. Corolla ca 1 cm long; lobes 5, remaining attached at apex to form a calyptra, and circumscissile at base, yellow. Stamens numerous, ca 215; filaments free almost to base, 5–10 mm long, yellow, apical portion tuberculate, the anthers small. Ovary globose-ellipsoid, ca 12-locular, glabrous on exterior. Styles 11–13, ca 1.5 mm long, glabrous. Fruit flattened-globose, ca 1.5 cm broad, 1 cm long, not conspicuously ribbed or pointed, 10–12-locular; exocarp glabrous, smooth; pericarp thick, hard, smooth, interior glabrous.

Additional material examined: COLOMBIA. AMAZONAS-VAUPÉS: Río Apaporis, between Rios Pacoa & Kananarí, 16.VIII.1951, fl., *Schultes & Cabrera 13561* (COL, GH, K, NY). CAQUETÁ: Araracuara, Quebrada El Engaño, 150-200 m, 21.XI.1991, fl.,

Restrepo & Matapi 535 (COAH, K). ECUADOR. NAPO: km 2 Cotundo-Cota, 1,130 m, -0.72800, -77.77200, 5.VIII.1984, fl., *Dodson et al. 15068* (MO). PERU. LORETO: Maynas, 21 km S of Iquitos, Allpahuayo, 120 m, -3.97111, -73.41888, 20.IX.1990, fl., *Pipoly et al. 12235* (K, MO). Jenaro Herrera, 04º53'98"S, 73º39'06"W, 3.X.2000, fl., *Pennington et al. 17031* (K, MOL), *V. Arostegui 66* (F, NY, S, US, WIS).

This species is easily recognised in the genus by the pilosity of the petioles, peduncles and inflorescences.

The species is present in Amazonian Colombia and Peru. Forests on high non-flooded ground.

Local names: Colombia: *gaw-gĕ* (Makuna), *ho* (Puinave); Peru: *espintana blanca, tabauri*.

2.9. *Anthodiscus trifoliatus* G.F.W. Meyer, Prim. F. Esseq. 194–195. 1818.
Anthodiscus guianensis Walpers, Rep. Bot. Syst. 1: 410 (1824), nom illegit.
Type: GUYANA. Rio Essequibo, Sophienburg Plantations, *Rodschied 251*, *Herb. G.F.W. Meyer 251* (holotype GOET000556). Fig. 9c

Tree to 30 m tall, usually much smaller, ca 10 m, young branches glabrescent. Leaves with stipules ca 2 mm long, triangular-lanceolate, intrapetiolar, persistent, trifoliolate; petioles 1–3 cm long, terete, glabrescent; leaflets shortly petiolulate, terminal petiolule 2–6 mm long, lateral petiolules shorter than the terminal one, petiolules glabrescent, shallowly canaliculate; stipels absent; the laminas oblong-elliptic, more or less symetrical, coriaceous, acuminate at apex, acumen 5–13 mm long, cuneate at base, crenate at margins, glabrous on both surfaces, terminal lamina 8–12.5 × 3.5–5 cm, lateral laminas smaller than the terminal one; midrib prominulous above; primary veins 9–12 pairs, plane above, prominulous beneath. Peduncles 1.5–2.5 cm long, terete, lenticellate, glabrous. Inflorescences elongate botryoids, ca 30 flowered; rachis 4–12 cm long, glabrescent, lenticellate; flowering pedicels 3–5 mm long, with 2 small, lanceolate, persistent, membraneous bracteoles. Calyx broadly cupuliform, ca 2.0 mm long, glabrescent on exterior, 5-pointed, margin ciliate. Corolla ca 5 mm long; lobes 5 but remaining attached at apex to form a calyptra, and circumscissile at base, greenish white in color. Stamens numerous, ca 270; filaments free almost to base, 5–10 mm long, white, apical portion tuberculate; anthers small. Ovary globose, 12-locular, glabrous on exterior. Styles 12, ca 1 mm long, glabrous. Fruit flattened-conical, ca 17 mm wide, 10 mm long at maturity, tapered to the apex, 12–15 ribbed, ca 12-locular; exocarp glabrous, ridged; pericarp thick, hard, ridged, interior glabrous.

Additional material examined: GUYANA. Moraballi Creek, Essequibo River, 14.IX.1939, fl., *Fanshawe 255 (F.D. 2991)* (K, NY, S). Demerara-Berbice, Fairview Landing, E bank Essequibo River, near end of Mabura Road, 4.66667, -58.6667, 19.IX.1990, fl. and fr., *McDowell 3265* (K, US). Cuyuni-Mazaruni, Wolga, 1 km S of Kamwatta Creek, Essequibo River, 1.IV.1993, fr., 6.45, -58.6, *Henkel et al. 1828* (K, US); Potaro-Siparuni, Essequibo R, 0.5 km N of Tiger Creek, 04º32'N, 58º35'W, 3.X.1996, fl., 3.X.1996, *Clarke 2765* (K, US).

Quite distinct by its acuminate leaves, its bracteoles, pedicels and lenticellate peduncles.

The species is endemic to Guyana. Low lying riverine forest.

Anthodiscus trifoliatus is listed as rare (R) in Walter & Gillett (1998).

Imperfectly known species

2.10. *Anthodiscus fragrans* Sleumer, Notizbl. Bot. Gart. Berlin 15: 375. 1941.
Type: ECUADOR. PASTAZA: Mera, Oriente, *H. Schultze Rhonhof 2926*; (holotype B, lost; isotype frag. K000432566).

This species is known only from the type which was lost at Berlin. The small fragment at Kew is insufficient to evaluate this species accurately. It is related to *A. klugii* and *A. trifoliatus* on account of the acuminate leaves, but the acumen is much shorter and blunter than that of *A. klugii*, and the leaves are thinner and smaller.

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