

A revision of neotropical *Diospyros* (Ebenaceae): part 7

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Abstract

In the course of a revision of New World Ebenaceae for "Flora Neotropica" and some regional floras, specimens from ca. 80 herbaria have been studied. The Caribbean *Diospyros revoluta* POIR., the Hispaniolan endemic *D. domingensis* (URB.) ALAIN (synonym: *D. leonardii* (URB. & EKMAN) ALAIN) and the Puerto Rican endemic *D. sintenisii* (KRUG & URB.) STANDL. are here described in detail. The Haitian endemic *D. oxycarpa* (URB.) ALAIN is here transferred as subspecies to *D. domingensis*. Lectotypes for *D. domingensis*, *D. oxycarpa*, and *D. sintenisii* are selected. Figures, distribution maps, and lists of specimens are included.

Key words: Ebenaceae, *Diospyros domingensis*, *D. leonardii*, *D. oxycarpa*, *D. revoluta*, *D. sintenisii*, *Maba*, revision, taxonomy, distribution maps, flora of the Caribbean area, Antilles.

Zusammenfassung

Im Rahmen einer Revision der neuweltlichen Ebenaceae für "Flora Neotropica" und einigen Regionalfloren konnten Herbarbelege aus ca. 80 Herbarien studiert werden. Die karibische Art *Diospyros revoluta* POIR., der Endemit Hispaniolas *D. domingensis* (URB.) ALAIN (Synonym: *D. leonardii* (URB. & EKMAN) ALAIN) und der Puerto-Ricanische Endemit *D. sintenisii* (KRUG & URB.) STANDL. werden hier im Detail beschrieben. Der Haitianische Endemit *D. oxycarpa* (URB.) ALAIN wird hier als Unterart zu *D. domingensis* gestellt. Lectotypen für *D. domingensis*, *D. oxycarpa* und *D. sintenisii* wurden ausgewählt. Abbildungen, Verbreitungskarten und Listen der gesehenen Herbarbelege werden ebenfalls präsentiert.

Introduction

In the Americas, the Ebenaceae are represented by the genera *Diospyros*, with about 100–130 species, and *Lissocarpa* with eight species. In the course of an ongoing revision of Ebenaceae (WALLNÖFER 2001a, 2001b, 2004a, 2004b, 2004c, 2006, 2007, 2008a, 2008b, 2009a, 2009b, 2010a, 2010b, 2010c, 2010d, 2011, 2012a, 2012b, 2013, WALLNÖFER & MORI 2002, ESTRADA & WALLNÖFER 2007; see also DUANGJAI et al. 2006, 2009) for "Flora Neotropica", "Flora of Ecuador", "Flora of the Guianas", and "Flora de Paraguay" several new species have already been described (WALLNÖFER 1999, 2000, 2003, 2005).

Note: Additions are given in brackets; coordinates given in brackets were determined during this revision; acronyms of herbaria according to THIERS (2013); data from herbarium labels are cited here in a standardized way; – abbreviations: defl = deflorate; fl = flowering; flbuds = with flower buds; fr = fruiting; st = sterile; yfr = with young fruits; carp = fruit in the carpological collection; n.s. = not seen; s.n. = without number; s.d. = without date; s.coll. = without collector; s.lat. = sensu lato; s.str. = sensu stricto; 2× = 2 sheets.

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Fig. 1: Lectotype of *Diospyros domingensis* (URB.) ALAIN subsp. *domingensis* [US].

Diospyros domingensis (URB.) ALAIN subsp. *domingensis*, Brittonia 20: 154 (1968), – [fig. 1–4].

≡ *Maba domingensis* URB., Symb. antill. 7 (3): 328–329 (1912).

Typus: Dominican Republic, Barahona, bei [near] Cabral, 30 m, [18°15' N, 71°13' W], (fl male), 10 Mar. 1911, **M. Fuertes 828** [holotype: B (destroyed), lectotype (here selected, fig. 1): US, isotypes: A, BM, BP n.s. (dig. photo), F, G, GH, HBG, K, L n.s. (dig. photo), LE, LIL n.s. (dig. photo), MO, S, U, WRSL, Z], "Baum [tree]"

= *Maba leonardii* URB. & EKMAN, Ark. Bot. 23A (5): 100–101 (1930).

≡ *Diospyros leonardii* (URB. & EKMAN) ALAIN, Brittonia 20: 154 (1968).

Typus: Haiti, Artibonite, Massif du Nord, Gros-Morne, between the town and Trois-Rivières, 250 m, [19°40' N, 72°41' W], alluvial soil (solo alluviali), (fl female), 22 Jun. 1927, **E.L. Ekman H 8518** [holotype: B (destroyed), lectotype (here selected, fig. 2): S, isotypes: EHH n.s., GH (fragm. ex US), K, LL, S (photo NY: N.S. 6904 at FHO, NY), US], "small tree; flowers white" and on the back of the handwritten label at S: "this plant (the very same tree!) was collected by Leonard"

Treelet or tree up to 8 m tall (already flowering when 2 m tall), with a trunk diameter up to 20 cm (Holdridge 2076), evergreen or semideciduous (as can be seen on the type collection), much-branched (Liogier 10901); branches spreading and drooping (Liogier 15209); **indumentum** consisting of simple, appressed or slightly spreading, straight or slightly flexuose, light or dark colored hairs of different length; twig apices densely hairy; scales of buds soon glabrescent; young twigs often slightly flattened, later on subterete, drying dark brown, soon glabrescent; older twigs gray or blackish-gray, slightly fissured, with some raised lenticels; **leaves** (fig. 3a) alternate, with brochidodrome venation; petioles 3–4 (–7) mm long, 1.5 mm thick, flat adaxially, light brown, glabrous, laterally winged up to the base; scars of the petioles markedly thickened; leaf lamina broadly lanceolate to elliptic, or less frequently obovate or ± circular, (2–) 3–9.5 cm long, (1–) 2–5 (–6.2) cm wide, (1–) 1.2–2 (–2.3) times longer than wide, widest usually in the middle, firmly chartaceous, glabrous (abaxially with scattered hairs along the midvein when very young), dull and gray on both sides (but sometimes brownish abaxially) when dry; leaf apex ± obtuse, less frequently rounded, or rarely emarginate; base of lamina cuneate, tapering into the petiole; leaf margins ± entire (sometimes minutely irregular), ± revolute, with a thickened but not flattened marginal vein; flachnectaria few (up to ca. 10), usually present on the proximal 1/3–1/2 of the abaxial leaf surface; venation usually lighter than the lamina; midvein flat or slightly sunken adaxially, markedly prominent abaxially, glabrous on both sides; secondary veins ca. 4–6 per side, prominent on both sides, the proximal ones acute-angled, ± straight and long (often well distanced from the others), the more distal ones ± obtuse-angled and arcuate; intersecondary veins inconspicuous; tertiary veins slightly raised on both sides and often ± markedly reticulate; quaternary veins not always visible; **inflorescences** arranged at the base or along the proximal part of new shoots in the axil of leaves (the lowermost ones often in the axil of very small leaves or sometimes in the axil of caducous bracts); male inflorescence units up to ca. 1.5 cm long, consisting of a simple, usually 3-flowered cyme (fig. 3b); peduncles 1–4 mm long, 0.6–0.8 mm thick, scattered hairy or ± glabrous; pedicels 1–2 mm long, ca. 0.5 mm thick, medium to densely hairy (hairs dark brown to blackish on Holdridge 2076); female cymes 1-flowered (fig. 3d); stalk (peduncle and pedicel) 2–6 mm long

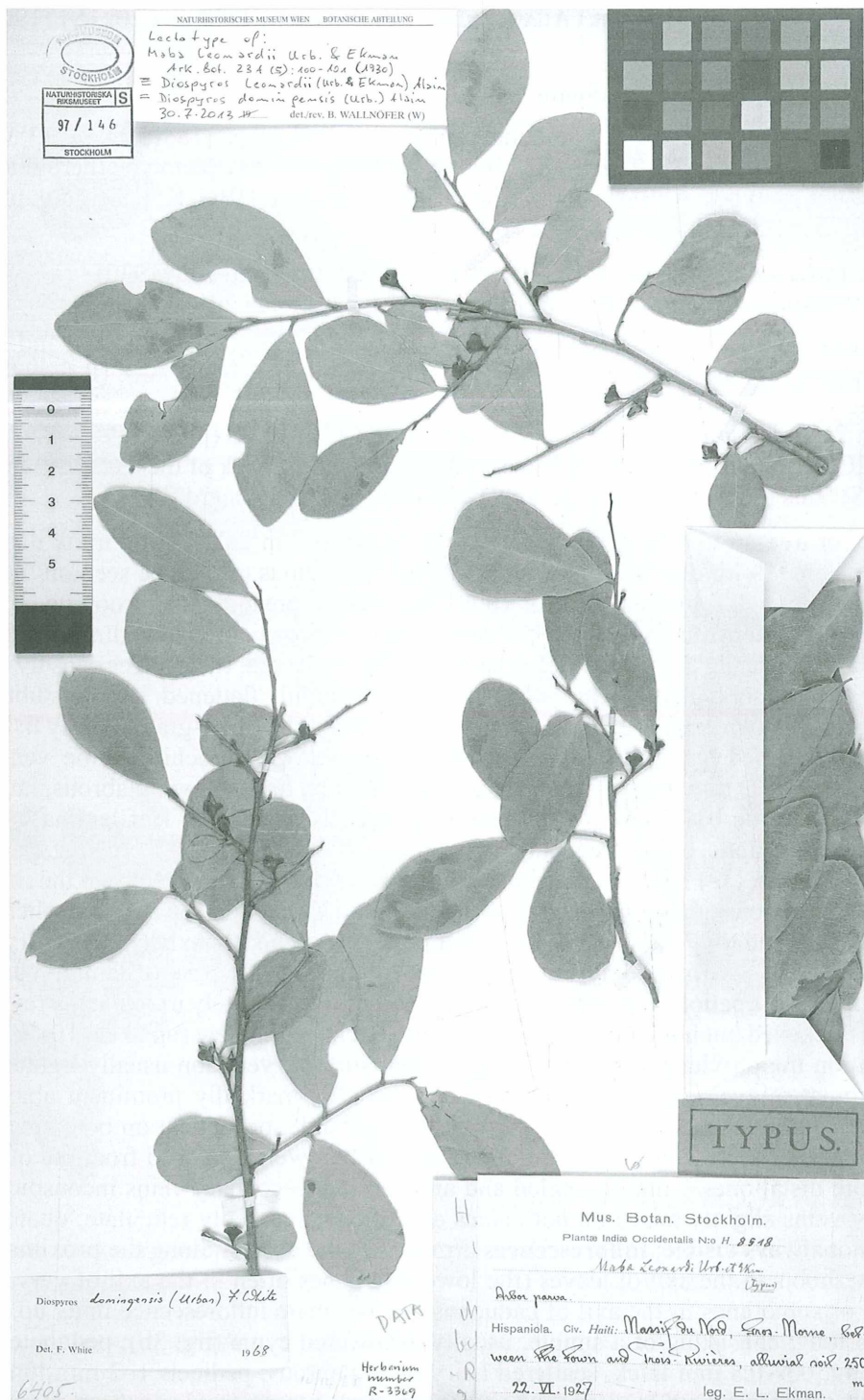


Fig. 2: Lectotype of *Diospyros leonardii* (URB. & EKMAN) ALAIN [S].

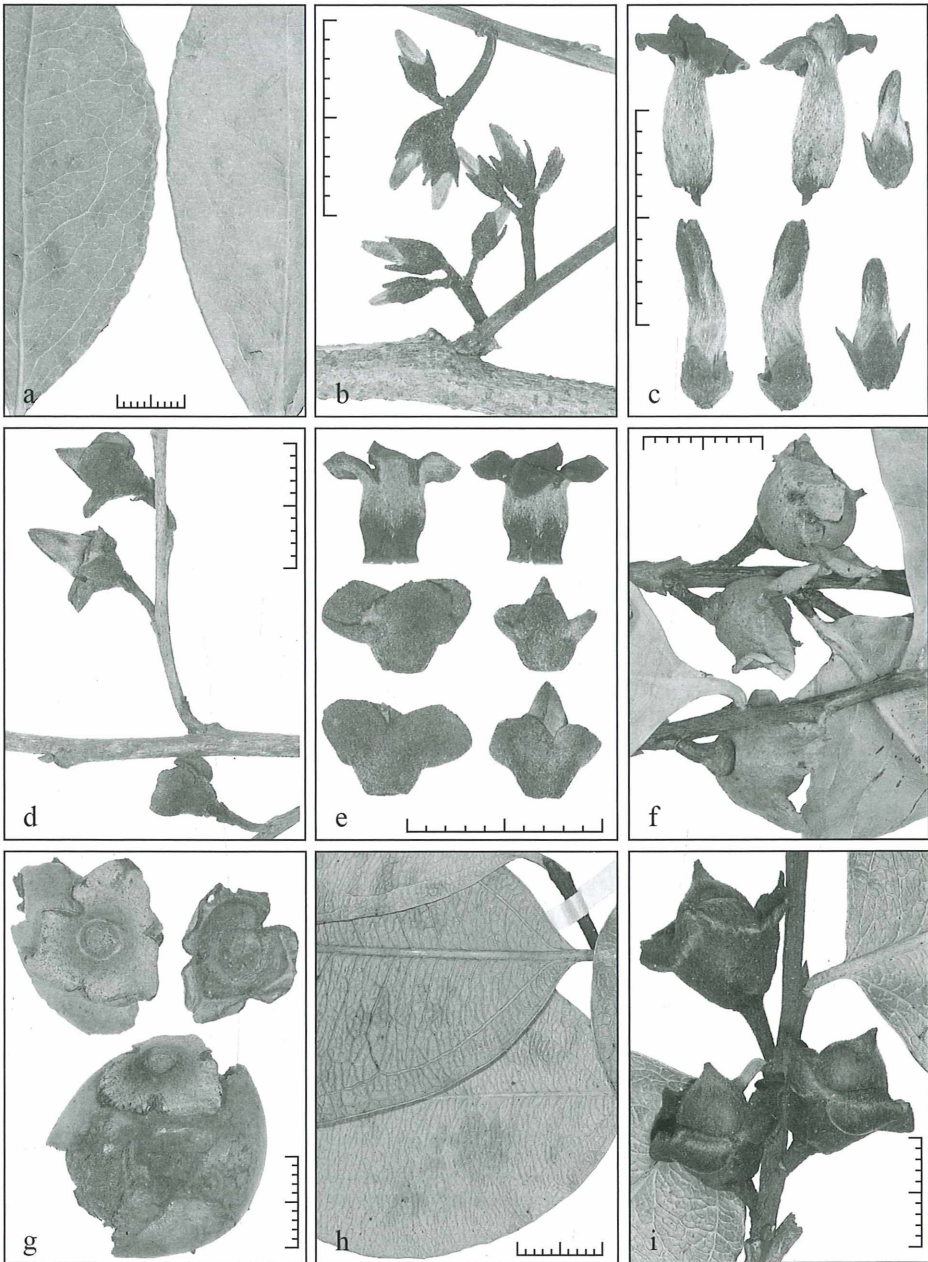


Fig. 3: *Diospyros domingensis* subsp. *domingensis*: a: abaxial (on the left side) and adaxial (on the right side) leaf surface; – b: male inflorescences; – c: male flowers; (a–c: from Fuertes 828, isotypes [at S, G and U, respectively]); – d: female inflorescences; – e: female flowers; (d–e: from Ekman H 8518, isotypes of *D. leonardii* [at S and LL, respectively]); – f: young fruits (from Fuertes 993B [A]); – g: fruit and calyces (right side on top: calyx as seen from the inside; from Bro. Alain = Liogier 10901 [NY]). — *D. domingensis* subsp. *oxycarpa*: h: leaf surfaces; – i: young fruits (both from Ekman H 4670, lectotype [S]); – scale = 1 cm.

and in the middle 0.8–1 (distally 1.5) mm thick, with same indumentum as on pedicels of male flowers; bracteoles of male and female flowers 1.3–2.5 mm long and 0.8–1.5 mm wide, \pm triangular, \pm glabrous, soon caducous; **flowers** 3 (–4)-merous; male flowers (fig. 3b–c) ca. 9 mm long (pedicels excluded) at anthesis; calyx ca. 3 mm long and wide, undivided in the proximal 1.5–2 mm, without longitudinal ridges, with scattered short, appressed hairs on the outside, glabrous inside; undivided part of the calyx cup-shaped; calyx lobes 1–1.5 mm long, 2 mm wide, \pm triangular, with a tuft of blackish hairs at the apex; margins of lobes flat; sinuses between the lobes inconspicuous; corolla ca. 8 mm long, white when alive (URBAN 1912); tube ca. 7 mm long, widest in or below the middle and there 1.5–2 mm wide, densely covered with long, appressed, straight, light, dark brown or blackish hairs outside, glabrous inside; throat narrow (ca. 1 mm wide); corolla lobes \pm ovate, ca. 4 mm long and 2 mm wide, \pm acute, densely covered with light, dark brown or blackish, short hairs abaxially, glabrous adaxially; stamens 12 (only one, 7.5 mm long flower bud of Fuertes 828 dissected), strongly differing in length, 2–4 mm long, solitary or some in pairs (the outer long and the inner one short), glabrous, adnate to the corolla tube near its base; filaments 0.5–1.5 mm long and ca. 0.2 mm wide, flat; anthers 1.5–2.5 mm long and ca. 0.3 mm wide, widest near base and there truncate, tapering into a ca. 0.3 mm long conical connective appendage distally; rudiment of the ovary consisting of an irregular, densely hairy lump of tissue, lacking stylodia; **female flowers** (Ekman H 8518, fig. 3d–e) ca. 8 mm long (pedicels excluded); calyx ca. 5 mm long and ca. 7 mm wide, undivided in the proximal 1.5–2.5 mm, on the outside medium densely covered (distally more scattered) with short, \pm appressed, light or dark hairs and with a tuft of minute, dark hairs at the apex of lobes; undivided part of the calyx broadly cup-shaped, glabrous inside; calyx lobes 3–3.5 mm long, 4–5 mm wide, \pm semicircular, sometimes emarginate or \pm acute (the latter on Mejía & Cabral 1766), with \pm involute margins, adaxially \pm densely covered with appressed hairs proximally and with spreading hairs distally; proximal half of the lobes adaxially with a gable-like, raised, densely hairy step (fig. 3g: right side on top); area around the sinuses between the calyx lobes slightly expanded and protruding outwards; corolla 6–7 mm long, white (Ekman H 8518); tube 4–4.5 mm long and ca. 3 mm wide, widest \pm in the middle, on proximal half not cylindrical (slightly deformed due to the internal shape of the calyx), medium densely to densely covered with long and short, appressed, straight, light hairs on the outside, glabrous inside and in the proximal $\frac{1}{3}$ – $\frac{1}{2}$ on outside; throat ca. 1.5 mm wide; corolla lobes 3–3.5 mm long and 3 mm wide at the base, acute, glabrous adaxially, on abaxial side densely hairy along the keel, scattered hairy towards the margins and there \pm glabrous; staminodia 3 (only one anthetic flower of Ekman H 8518 dissected), antesealous, 3 mm long, glabrous, adnate at the base of the tube; filaments ca. 1.8 mm long and ca. 0.2 mm wide, free in the distal half; antherodes flat, lanceolate, ca. 1.2 mm long and 0.3 mm wide; ovary 6-locular, as a whole 4 mm long, ca. 2 mm in diameter below the middle, tapering into the ca. 1.5 mm long, conical style, densely covered with appressed, straight, light hairs; stylodia 3, fused together up to the apex, densely hairy; stalk of the **fruits** up to 6 (–8) mm long, up to 2 (distally 3–4) mm thick; fruits (fig. 3f–g) up to 6-seeded, \pm globose, up to ca. 2.5 cm in diameter, yellowish when alive (as stated on three collections of Liogier), brown, smooth and with tightly adhering epidermis when dry, with scattered, long, \pm appressed hairs when young, glabrescent except at the apex when maturing, distally with the mucro-like remnant of the style, detaching with the calyx; fruit wall with a stone cell layer, ca. 0.5 mm thick when dry; calyx on young

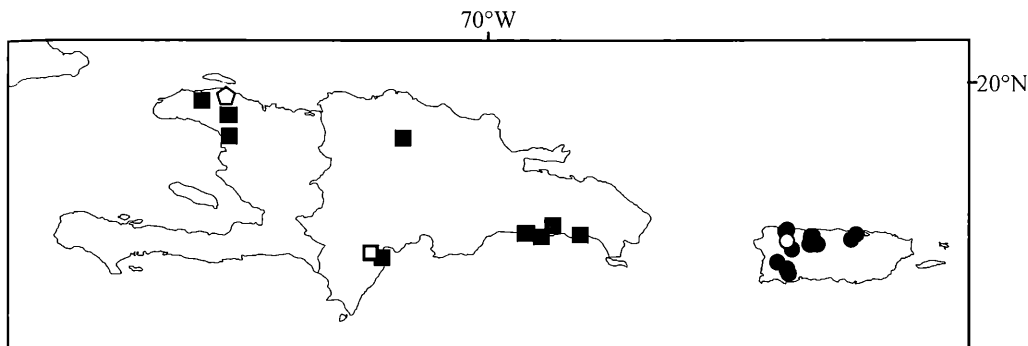


Fig. 4: Distribution of *Diospyros domingensis* subsp. *domingensis* (■, type locality: □). — *D. domingensis* subsp. *oxycarpa* (△). — *D. sintenisii* (●, type locality: ○).

fruits cup-shaped (Fuertes 993B, fig. 3f), later on ± dish-shaped, as a whole up to 1.5 cm wide and ca. 0.5 cm high, glabrescent on the outside; area around the sinuses between the calyx lobes only slightly expanded and protruding outwards (irregularly protruding inwards on young fruits of Fuertes 993B); sinuses often longitudinally split on maturing fruits; undivided (basal) part of the calyx ca. 3 mm wide when intact, without longitudinal ridges running down from the sinuses abaxially; proximal half of the calyx on its inside forming an elevated, triangular platform with convex edges tightly appressed to the fruit, glabrous proximally and appressed hairy distally; lobes ca. 4 mm long and 8 mm wide, on some plants obtuse, on others acute, involute, with ± raised longitudinal veins abaxially, only slightly apposed to the fruit or horizontally spreading, still covered with remnants of the indumentum adaxially; seeds ± formed like the segments of an orange, ca. 12 mm long, 8 mm wide, 6 mm thick, brownish when dry; outer tangential (periclinal) wall of the exotestal cells finely striate below the surface; endosperm ruminant.

Distribution, habitat and phenology: It is known only from the island of Hispaniola (Haiti and the Dominican Republic), (fig. 4). Collectors reported it from thickets and woods on limestone. The soil was described as dry and rocky. LIOGIER (1989) stated: "en maniguas sobre rocas" [in thickets on rocks]. CANO & VELOZ (2012) listed it as a member of the xeric "Zamia debilis-Metopietum toxiferi secondary forest" which grows on porous coral substrate in the east of the country. – It was collected from sea level up to elevations of 400 meters, and was found in flower in February, March, May and June, and in fruit from February to May.

Vernacular names: cocuyo (LIOGIER 1989, Scarff 8E and 17).

Specimens examined: **Haiti**, Nord-Ouest, Presqu'île du Nord-Ouest, Port-de-Paix, Carreau Dartis [on original-label], " Carreau-Datty, in the foothills on the road to Haut-Moustique" [on the other label], [ca. 19°49' N, 72°58' W], (st), 14 Jul. 1925, **E.L. Ekman ser III. H. 4564** [EHH n.s., LL, S, US], "medium sized tree, sterile"; – Artibonite, along lane to Trois Rivières W of Gros Morne, 235 m, [19°40' N, 72°42' W], dry soil, (fr), 18 Feb. 1926, **E.C. Leonard 9892** [FHO (fragm.), GH 2×, NY, UC, US 2×], "tree 20 ft. high" and "probably from type tree: Ekman 8518"; – Gonaives, 20 m, [19°27' N, 72°41' W], (fl male), 18 Feb. 1945, **L.R. Holdridge 2076** [G, NY, US], "tree 8 m tall, 2 dm dbh"

Dominican Republic, Santiago, Jaiqui Picado, limestone hills 20 miles W of Santiago, 300–400 m, [19°26' N, 70°53' W], in thickets near the bottom of a gorge, (fr), 14 May 1969, **Bro. (Brother) Alain (= E.E. Liogier) 15209** [NY, P], "small tree up to 6 m; branches spreading and drooping; fruit yellowish"; – Barahona, bei

Barahona, [18°12' N, 71°06' W], (yfr), 1911, **M. Fuertes 993B** [A]; – Distrito Nacional, 1,5 km W de Boca Chica, frente a la playa de Andres, 5 m, [18°27' N, 69°37' W], zona dedicada a potreros, (flbuds female), 29 May 1986, **M. Mejía & M. Cabral 1766** [FHO, JBSD n.s. (dig. photo), MO, NY], "arbolito 4 m; botones florales verde; frutos viejos goteados; algo común en el lugar"; – Boca Chica, [18°27' N, 69°36' W], coastal thickets, on limestone, (fr), 17 Apr. 1968, **Bro. (Brother) Alain (= E.E. Liogier) 10901** [GH n.s., NY, P], "shrub 3 m high, much branched; fruits yellowish"; – Boa Chica [= Boca Chica], [18°27' N, 69°36' W], in thickets, (fr), 14 Mar. 1964, **Bro. (Brother) Augusto (= B. Lavastre) 1393** [A, NY (+ carp.)], "tree 2–3 m"; – San Pedro de Macorís, Guayacanes, [18°25' N, 69°27' W], rocky soil, (fr), 2 Feb. 1963, **Bro. (Brother) Augusto (= B. Lavastre) 606** [NY], "shrub 2 m"; – ubicado al norte del Río Higuamo [= Río Macorís], en uno de los potreros de los Vicini, [ca. 18°32' N, 69°20' W], vegetación asociada: *Eugenia*, *Citrus aurantiifolia*, *Haematoxylon campechianum*, (yfr), 20 Mar. 2011, **R. Sanó I** [JBSD n.s. (dig. photo)]; – La Romana, Cumayasa, La Romana, 20–30 m, [18°26' N, 69°3' W], en bosque sobre rocas calcáreas, (fr), 7 Apr. 1973, **Bro. (Brother) Alain (= E.E. Liogier) & P. Liogier 18899** [NY], "arbolito 3–4 m; ramas extendidas; frutos amarillentos"; – without any locality, (st), 1936, **J.G. Scarff 17** [WIS (MAD)]; – (st), 1938, **J.G. Scarff 8E** [F, FHO, WIS (MAD)].

***Diospyros domingensis* (URB.) ALAIN subsp. *oxycarpa* (URB.) B.WALLN. comb.n.**, – [fig. 3h–i, 4–5].

≡ *Maba oxycarpa* URB., Ark. Bot. 23A (5): 101–102 (1930).

≡ *Diospyros oxycarpa* (URB.) ALAIN, Brittonia 20: 154 (1968).

Typus: Haiti, Nord-Ouest, Massif du Nord, St.-Louis du Nord, Morne Baron, top of the mountain, 950 m, [ca. 19°52' N, 72°43' W], hard limestone (eocene limestone – "solo dure calcario"), (yfr), 19 Aug. 1925, **E.L. Ekman H 4670** [holotype: B (destroyed), lectotype (here selected, fig. 5): S, isotypes: EHH n.s., GH (fragm. ex US), K, NY, S, US 2×], "medium-sized tree (arbor mediocris)"

This subspecies is only known from the type collection which was gathered at a higher elevation (950 m). It differs from *D. domingensis* s.str. by the black drying bark of young twigs, the scattered, appressed, brownish-black hairs especially on the abaxial side of the midvein of mature leaves, and the more dense, dark brown to brownish-black indumentum on fruits and peduncles. The tertiary venation along the midvein of leaves is somewhat more thickened, long, ± straight, ± parallel, and markedly obtuse-angled. Further material is needed to ascertain whether or not this taxon may represent really a distinct entity. In the worst case it could just represent a somewhat anomalous individual of *D. domingensis*. As the woods in Haiti seem to have been ± completely destroyed in the meantime, it is doubtful if any populations of this plant still persist.

***Diospyros revoluta* POIR.**, Encycl. (Lamarck) 5: 435 (1804), – [fig. 6–8].

Typus: Montserrat, [ca. 16°44' N, 62°12' W], (fl female), 1778, **J. Ryan s.n.** [holotype: P-JU (fig. 6); isotypes: BM (photo: A), C 3× (photos: A and in HOWARD 1961)].

Note 1: The holotype bears the writings: "amer. merid." and written by another hand: "misit D. Vahl 1797" The protologue states: "Cette plante est originaire de l'Amérique méridionale. Elle a été communiquée par M. Vahl à M. Jussieu. (V. s. [= vidi sicco] fruct. [correct is: fl.] in herb. Juss.)" Two of the isotypes pertaining to the herbaria F.M. Liebmann and H.C.F. Schumacher which are now kept in C, have to date not been identified as such. They bear three different names (*D. revoluta*, *mutans* and *obovata*) which obviously were written before the name *D. revoluta* was validated. Both have

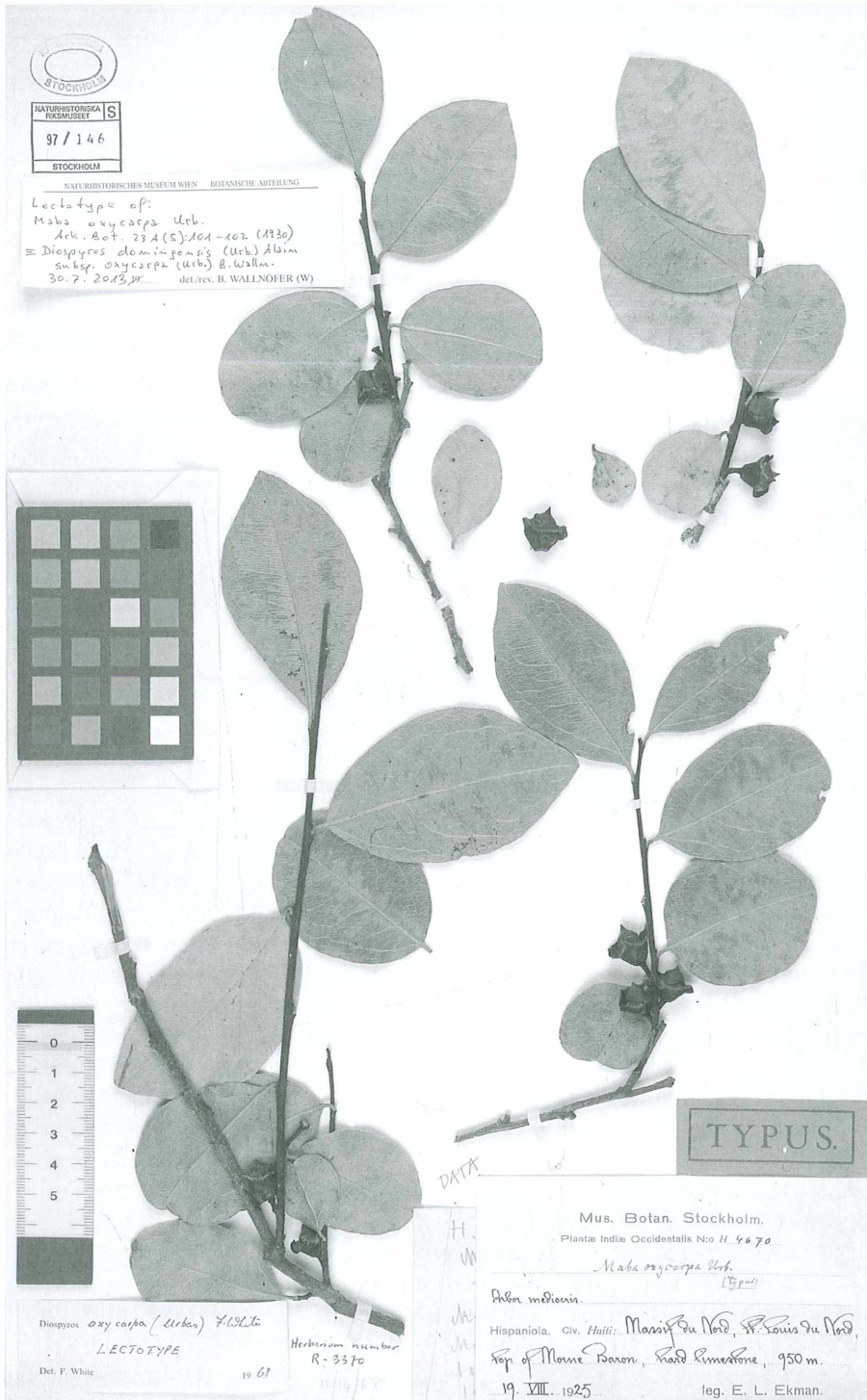


Fig. 5: Lectotype of *Diospyros domingensis* (URB.) ALAIN subsp. *oxycarpa* (URB.) B. WALLN. [S].

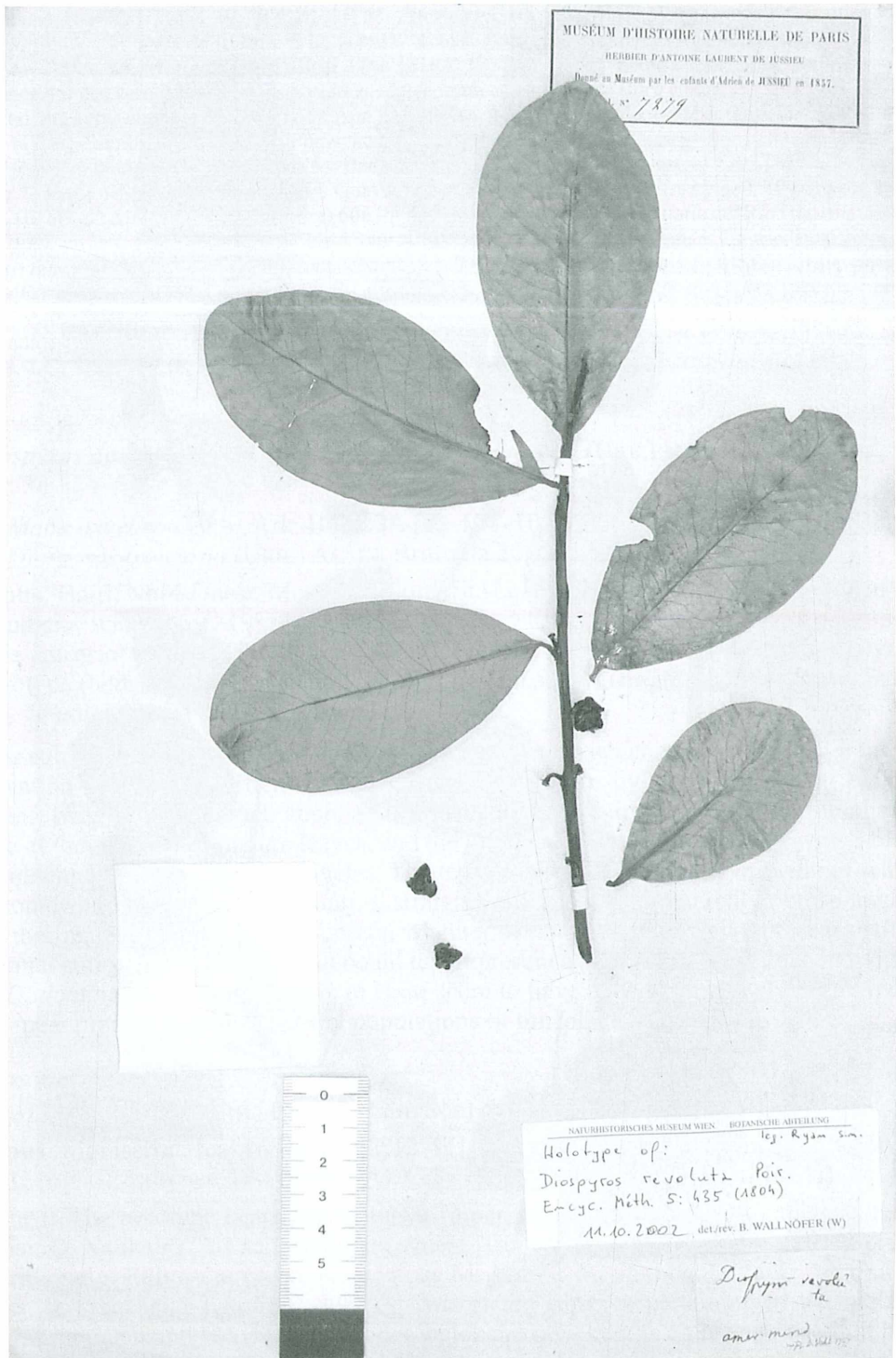


Fig. 6: Holotype of *Diospyros revoluta* POIR. [P-JU].

been annotated by A.J.G.H. Kostermans [who worked on Asian Ebenaceae] in 1975 as "*Diospyros nutans*" [? – not *D. nutans* KING & GAMBLE, published in 1906, and occurring on the Malay Peninsula].

Note 2: The illegitimate name *D. ebenaster* RETZ. had been applied by HIERN (1873) to four species: the Sri Lankan *D. ebenum* J.KÖNIG ex RETZ., the Central American *D. nigra* (J.F.GMEL.) PERR. [= *D. digyna* JACQ.; regarding this name change see TURNER 2013], the Antillean *D. revoluta*, and the Brazilian *D. brasiliensis* MART. ex MIQ. In 1915, SCOTT discussed all the existing literature concerning "*D. ebenaster*", but he did not become aware of the confusion of species. He came to the conclusion that it is a native plant of the West Indies. It was, however, HOWARD (1961) who realized the mix-up of species and who disentangled at least the first three of them. In a later paper important typifications were made (HOWARD & NORLINDH 1962).

Tree up to ca. 25 m tall (already flowering when 4–5 m tall), with a trunk diameter up to 1 m (Barrier 3215, 5441A) or even 1.5 m (IMRAY et al. 1909), evergreen; trunk and branches black (Howard et al. 18980, and many other collections); wood yellow (Duss 2573, Sastre et al. 2703, Barrier 3613, Nicolson 2132, Ernst 1364) or white (Stijfhoorn et al. 848); inner bark yellow (Howard et al. 19858), with orange juice (Howard & Howard 15104); **indumentum** consisting of two-armed (proximal arm extremely short or up to ca. a fifth of the length of the distal arm) or simple (but usually attached laterally), appressed or sometimes ± spreading, straight or slightly flexuose hairs of different length; twig apices densely covered with appressed, ± straight, light brown to ferruginous hairs; young twigs subterete, often ± flattened below leaf-insertions, soon glabrescent, drying dark brown to black; older twigs brownish or gray, soon longitudinally fissured and sometimes markedly gray-streaked; **leaves** (fig. 7a) alternate, with brochidodrome venation; petioles 3–6 (–8) mm long, ca. 2 mm thick, winged laterally ± to the base, ± flat or slightly sulcate adaxially, ± glabrescent; leaf lamina obovate (on proximal parts of new twigs) or ± elliptic (on distal parts of new twigs), (2–) 7–15 (–18.5) cm long, (1.5–) 3.5–6 (–9.6) cm wide, (1.2–) 1.8–2.7 times longer than wide, widest in the distal half, rarely in the middle, firmly chartaceous, usually glabrous on both sides (rarely with some remote, appressed hairs when young), dark green and glossy adaxially, lighter green abaxially when alive (Trejo-Torres et al. 1778, Jérémie 1211), glossy adaxially, dull abaxially and greenish gray or sometimes blackish on both sides when dry; leaf apex usually broadly rounded, less frequently obtuse, rarely emarginate; base of lamina cuneate, wing-like tapering into the petiole; leaf margins entire, revolute, with a light, ± sharp border; flachnectaria minute, few to ca. 20 on the proximal ½ of the abaxial leaf surface, rarely also present towards the leaf-apex (but Ekman 4595 with numerous tiny flachnectaria all over the surface); midvein shiny yellow when alive (Stijfhoorn et al. 848, Trejo-Torres et al. 1778), on adaxial side usually sunken (rarely at least partially ± flat), slightly raised distally, on abaxial side markedly prominent; secondary veins up to ca. 10 per side, prominent on both sides; intersecondary veins not conspicuous; tertiary and quaternary veins only slightly raised on both sides; area in-between the veinlets flat on both sides; **inflorescences** usually arranged at the base or along the proximal part (in the middle on Stahl 872) of new shoots in the axil of leaves (the lowermost ones often in the axil of very small leaves or sometimes in the axil of caducous bracts); male inflorescence units (fig. 7b) ca. 3 cm long, consisting of a simple, usually 3-flowered cyme (but ramified and with up to ca. 9 flowers in Nicolson 4239; for details see

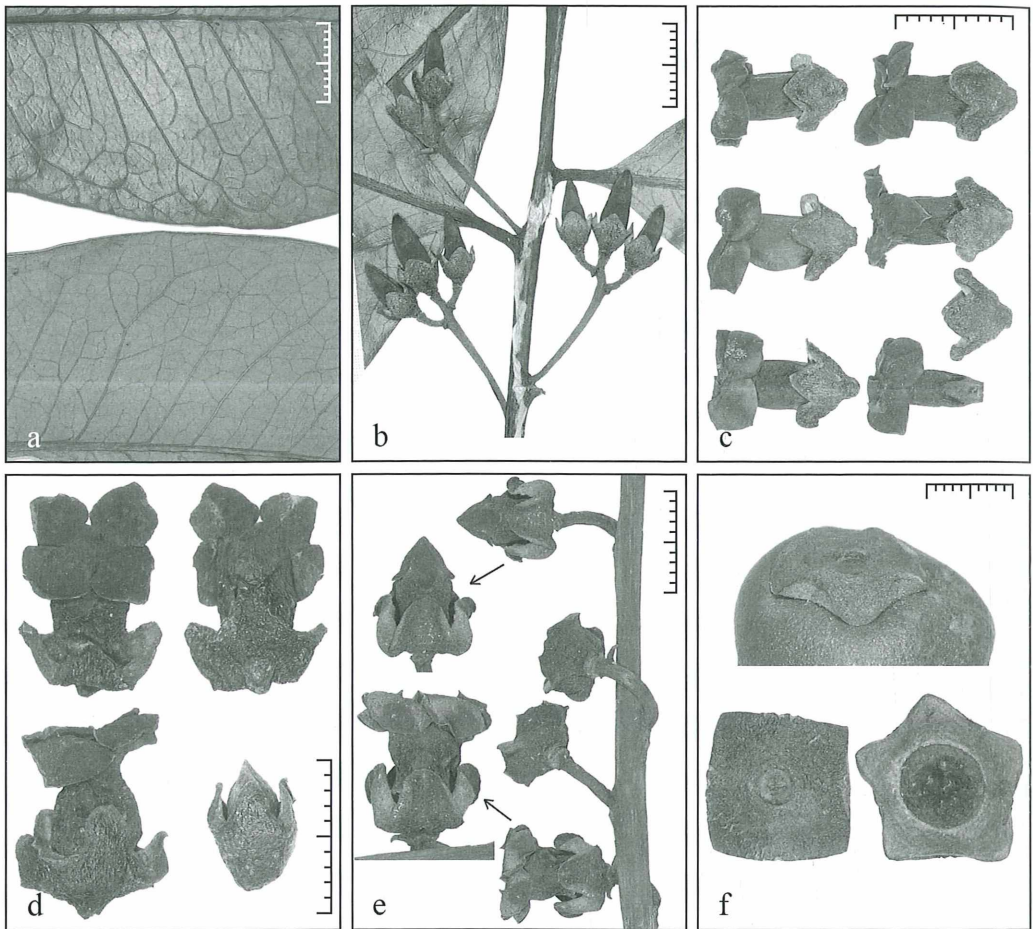


Fig. 7: *Diospyros revoluta*: a: adaxial (on top) and abaxial (on bottom) leaf surface (from Stijfhoorn et al. 848 [NY]); – b: male inflorescences; – c: male flowers; (b–c from Proctor 21068 [at US and A, respectively]); – d: male flowers (from Stahl 872; flower on top as seen from both sides [Z], two flowers on bottom [S]); – e: female inflorescences and flowers (from Ryan s.n., isotype [C]); – f: fruit and calyces (on top: from Ramage s.n. [K]; on bottom: two calices from Nicholls 24.2.1892 [K], on left side: 4-merous as seen from the outside, on right side: 5-merous as seen from the inside); – scale = 1 cm.

WALLNÖFER 2007: 226 and fig. 8d); peduncles up to 25 mm long, 1 mm thick, with scattered appressed, short, often thick and flattened hairs; pedicels 2–4 mm long, ca. 1 mm thick, denser hairy; female cymes 1-flowered (fig. 7e); stalk (peduncle and pedicel) 3–7 mm long and 1.5 mm thick, with same hairs as on male flowers or glabrescent; bracteoles at the base of the calyx; bracts and bracteoles of both sexes similar in shape, 1–2 mm long and ca. 1 mm wide, ± triangular, acute, hairy on both sides (less densely adaxially), soon caducous; **flowers** 4 (–5)-merous (according to Nicolson 4136, 4–6-merous); male flowers (fig. 7b–d) up to 9–13 mm long (pedicels excluded; largest flower buds 15 mm long), emanating a strong, fragrant smell (Duss 2573, Proctor 21068, Barrier

3692), pendent (Webster 13473); calyx 5–6.5 (–7) mm long and ca. 6 mm wide, undivided in the proximal 3–4 mm, sometimes with a longitudinal ridge running down from the sinuses abaxially, scattered hairy on the outside, densely covered with longer, straight, brown to ferruginous-brown hairs inside; calyx lobes 3–5 mm long, 4–6 mm wide, ± triangular, obtuse or broadly rounded, revolute (flexed towards the outside) proximally, densely covered (especially distally) with spreading hairs along the margins; sinuses between the lobes moderately expanded and protruding outwards (less than in female flowers); corolla 8–11 mm long, white (Duss 2573, Ernst 1364, 1831, Webster 13473) or cream (Proctor 21068, Barrier 3692), glabrous or with scattered, small, appressed hairs especially below the lobes on the outside, glabrous inside; tube 7–10 mm long, widest in or below the middle and there 4–5 mm wide; corolla throat very narrow (like a hole, see fig. 7d: left side on top), ca. 0.5 mm wide; corolla lobes broadly ovate, ca. 4 mm long and ca. 5 mm wide, obtuse; stamens 12 (one flower of Proctor 21068 dissected) or 16 (one flower of Webster 13473 dissected; this number is also indicated by Barrier 3692), usually in pairs, glabrous, differing in length, 3–5.5 mm long, adnate to the corolla tube near its base; filaments 0.5–2 mm long and ca. 0.2 mm wide, flat; anthers 2–3.5 mm long and ca. 0.8 mm wide, widest in the proximal third, cordate proximally, tapering into a short, conical connective appendage distally; connectives especially on abaxial side ± densely covered with appressed, straight hairs (less frequently with only few hairs); rudiment of the ovary consisting of a densely hairy lump of tissue, lacking stylochia; **female flowers** (fig. 7e) 7–8 mm long (pedicels excluded); calyx ca. 6 mm long and 8 mm wide, undivided in the proximal ca. 3 mm, scattered hairy on the outside, densely, ferruginous-brown hairy on the inside, with or without a longitudinal ridge running down from the sinuses abaxially; calyx lobes up to 4.5 mm long, 6 mm wide, ± broadly triangular, obtuse or broadly rounded, revolute (flexed towards the outside) proximally, densely covered with spreading hairs along the margins; area around the sinuses between the calyx lobes markedly expanded and protruding outwards; corolla yellowish (Howard & Howard 15117, Jérémie 1211) or yellow (Graveson & Smith 1137) when alive, ca. 7 mm long, tube ca. 6 mm long and ca. 4 mm wide, barrel-shaped, widest ± in the middle, scattered to medium densely covered (except at base) with minute hairs on the outside, glabrous inside; corolla throat ca. 0.5 mm wide (like a hole); corolla lobes ca. 6 mm long and 5–6 mm wide, ± semicircular or ± obtuse, auriculate at base, glabrous on both sides (except at the base on the outside); staminodia 8 (only one older flower bud of Jones 2956 dissected [flower buds of Britton 8508 and Howard & Howard 15117 proved to be abnormal and probably galled]), ca. 4.5 mm long; filaments 2–3 mm long, completely fused with the corolla tube, glabrous; antherodes ca. 1 mm long and ± 0.3 mm wide, free, flat, ± lanceolate, widest near base, glabrous or with some long hairs on the adaxial side, one of them quite long (2 mm), very narrow (0.2 mm) and tapering into a long tip distally; ovary 8 (–10)-locular, as a whole ca. 5 mm long, ca. 3 mm in diameter, tapering into the ca. 2 mm long style and stylochia, densely covered with long, appressed or slightly spreading, ± straight ferruginous-brown hairs; stylochia 4, ca. 0.5 mm long; stalk of the **fruits** 3–7 mm long, 1.5–2.5 mm thick proximally and 3 mm thick distally, still covered with old indumentum; fruits (fig. 7f) up to 8 or 10-seeded, ± globose, 5 cm in diameter when mature (Beard 432, Howard & Howard 15117, Barrier 3613), green and glossy when unripe, purple (Howard & Howard 19675) when ripe, black when old (Howard et al. 18980), with the epidermis adhering when dry, distally with the mucro-like remnant of the style, ± smooth or with a ± granulate surface (with subepidermal

stone cell granules) when dry; maturing fruits \pm glabrescent except at the apex; fruit wall with a stone cell layer, 1–2 mm thick when dry; calyx as a whole up to 2.5 cm wide and up to 0.5 cm high, up to 1.8 mm thick, containing many stone cell granules, black when alive (Sastre et al. 2703), scattered hairy on the outside, densely covered with appressed, ferruginous-brown hairs on the inside, usually forming a nearly quadratic (rarely five-lobed) plate (fig. 7f) which is appressed like a flat bowl to the fruit and detaches with it; area around the sinuses between the calyx lobes bent step-like downwards (fig. 7f: on top), ca. 3 mm thick; undivided (basal) part of the calyx 4 mm wide, without or with only faint longitudinal ridges running down from the sinuses abaxially; lobes 8 mm long and 11–13 mm wide, \pm flat and appressed to the fruit; seeds \pm bean-shaped, 13–16 mm long, ca. 7 mm wide, 4–6 mm thick, brown when dry; outer tangential (periclinal) wall of the exotestal cells finely striate below the surface; endosperm not ruminant.

Notes: Unfortunately, *D. revoluta* and *D. nigra* (= *D. digyna*; regarding this name change see TURNER 2013) were mixed up by the monographer of the family (HIERN 1873) and subsequent authors under the name "*D. ebenaster*". The resulting mixture of characters and dimensions has been still perpetuated (or copied) at least partially until recent times. For instance, the leaves of *D. revoluta* are said to be 6–30 cm long and the petioles 5–12 mm long (LIOGIER 1989, 1995); leaves 6–20 cm and petioles 5–20 mm (HOWARD 1989); leaves (6–) 7.5–20 (–30) cm and petioles 5–20 mm (FOURNET 2002). According to herbarium specimens available for study, the leaves of *D. revoluta* are, however, very rarely exceeding 15 cm in length and the petioles are only 3–6 (rarely up to 8) mm long! It is *D. nigra* (= *D. digyna*) which has longer petioles and leaves. The fruits of *D. revoluta* are said to reach 5–7 cm in diameter and to become black when ripe (HOWARD 1989), but these characters too belong to *D. nigra* (= *D. digyna*).

Data from literature regarding the habit can often not be assigned with certainty to any of the two species. The information (here translated) given by DUSS (1897) applies, however, to genuine *D. revoluta*: "trunk often more or less tortuous; with horizontally spreading branches; wood very bitter and hard, dark gray, hardly putrescible; bark black and strongly fissured (cracked) and detaching in plates; leaves shiny, the mature ones obovate, the young ones elliptic; flowers white; fruits depressed-globose containing 2–4 seeds; fruit pulp blackish" This information has been copied later at least partially by SASTRE & BREUIL (2007) and FOURNET (2002). LITTLE et al. (1974) give us the following information: evergreen tree to 80 feet [ca. 24 m] high and two feet [61 cm] in trunk diameter; with slight enlargements or buttresses at base (see for this also GRAVESON 2012); bark blackish, finely fissured and peeling off, exposing gray beneath; the inner bark light yellow, bitter and with a thin blackish layer; heartwood blackish and hard; petioles 0.25–0.5 inches [0.6–1.3 cm] long [mix-up with *D. nigra* (= *D. digyna*)]; lamina 2.5–7 inches [6.3–17.8 cm] long and 1.37–3 inches [3.5–7.6 cm] wide, shiny green adaxially, dull green abaxially; flowers fragrant; corolla white, 4-lobed; fruits: large pulpy berries, 1.25 inches [3.2 cm] in diameter. According to these authors, *D. nigra* (= *D. digyna*) "differs in having oblong-lanceolate leaves evenly tapered at both ends or rounded at base and short-pointed at apex, also larger edible fruits about 2 inches [5 cm] in diameter"

IMRAY et al. (1909) reported the tree to be large, the trunk 4 to 5 feet [1.22–1.52 m!] in diameter, and the wood tough and strong. NICOLSON (1991) describes the bark as dark and scaly. – The mature fruits are purple (Howard & Howard 19675). They may be eaten

and the seeds dispersed by bats. Nicolson wrote on his herbarium label numbered 4136: "fruit popular with birds but considered poisonous"

The only collection from Haiti available for study (Ekman 4595) is sterile. The short-petioled, obovate leaves are displaying a large quantity of minute flachnectaria scattered all over the abaxial surface! Fertile specimens from this country are needed for study!

The leaves of several collections (e.g., Proctor 21068) are infected and show characteristic galls.

Figures: male inflorescence, branch with fruits and leaves (LITTLE et al. 1974: fig. 648 [same plate reproduced in FOURNET 1978: fig. 682, 2002: fig. 72.2, LIOGIER 1989: fig. 170-2]); color photos of the trunk, leaves, a female flower bud and fruits can be seen in GRAVESON (2012), and two more pictures in USDA (2013).

Distribution and phenology: It is known from western Hispaniola (Haiti), Puerto Rico, and the Lesser Antilles (Montserrat, Guadeloupe, Marie Galante, Dominica, St. Lucia), (fig. 8). In Haiti it is reported to grow in the area of Port de Paix, St. Louis du Nord, Morne Chabre, and Les Roseaux (URBAN 1930, MOSCOSO 1943, LIOGIER 1989). Unfortunately, only one sterile collection from that country was available for study. No collections from the Dominican Republic have been reported in literature. In Puerto Rico it has been found in the Northern Limestone Hills (Arecibo), and in the Río Abajo Forest Reserve (AXELROD 2011). According to LITTLE et al. (1974), it grows also on the island of St. Kitts. It was collected from sea level up to elevations of 600 meters (1000 meters in Haiti). – In Puerto Rico it was collected in flower in January and June, and in fruit in January and April. LITTLE et al. (1974) reported it to be flowering there in spring,

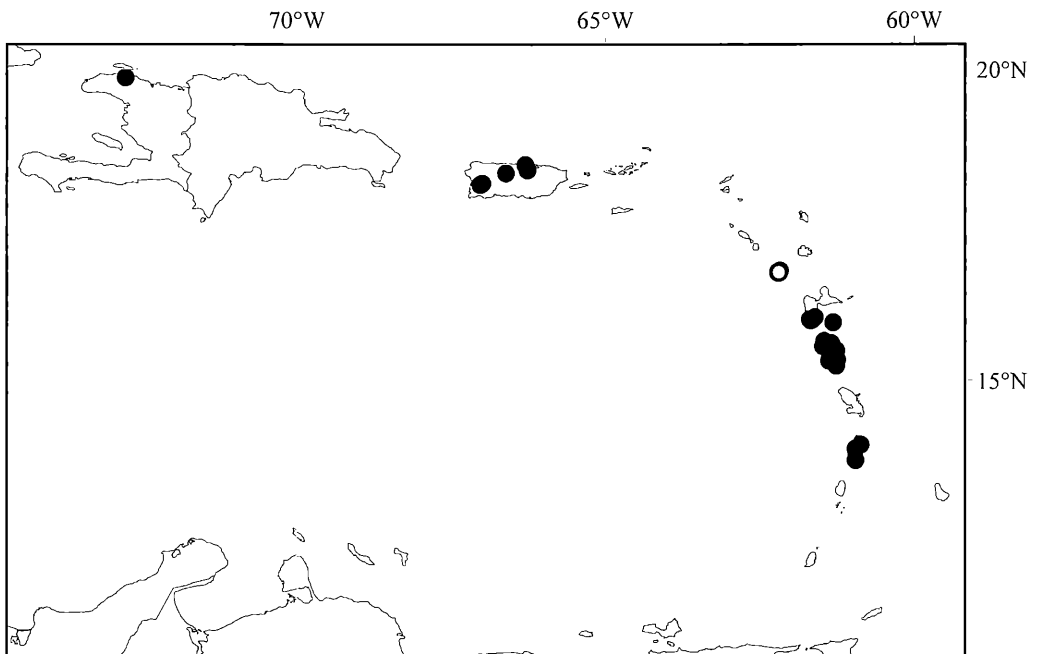


Fig. 8: Distribution of *Diospyros revoluta* (●, type locality: ○).

and fruiting in summer, and AXELROD (2011) indicated it to be fruiting in January and February. In Montserrat it was found in flower in January, and with fruits from January to March and in November. In Guadeloupe it was collected in flower from the end of May till July and in October, and with fruits in April and July. According to DUSS (1897), it is flowering there from June to August (repeated also by FOURNET 2002). In Dominica it was found flowering from April to July and in November, and fruiting from January to April and in June. In St. Lucia it is flowering in August and October, and fruiting in January.

Habitat: It grows in primary and secondary forests. In Puerto Rico it was collected in coastal forests, in riparian vegetation (moist forest), on mogote slopes and on serpentine soil (the later: Cedeño & Acevedo-Rodríguez 388). According to LITTLE et al. (1974) it is "rare in moist coastal, limestone, and lower Cordillera forests from sea level to 2000 feet [ca. 600 m] altitude" HOWARD (1989) annotated: "the trees on Montserrat are often free-standing in cultivated fields and obviously saved in clearing operations" FOURNET (2002) reported it in Guadeloupe from the "forêt xéro-mésophile, forêt mésophile, horizon inférieur de la forêt hygrophile" On the nearby island of Marie Galante it is quite common (Barrier 5441A). In Dominica it is said to be "common throughout dry woodlands" (Hodge & Hodge 3282) and was found in mesophytic woodland, in "transitional forests (between xerophytic and mesophytic zones)" (Hodge & Hodge 2676), in "scrubby, windswept coastal vegetation" (Hodge & Hodge 3177) but often also in secondary rainforests. In St. Lucia it has been collected in mesophilous forests but also on an "exposed, well-drained ridgetop with low tree canopy" (Graveson & Smith 1137).

Vernacular names: **Puerto Rico:** guayabota (STAHL 1888: 284, URBAN 1910, BRITTON & WILSON 1925, OTERO et al. 1945, LITTLE et al. 1974, LIOGIER 1995, AXELROD 2011, ACEVEDO-RODRÍGUEZ & STRONG 2012). – **Montserrat:** black apple (HOWARD 1961, LITTLE et al. 1974, indicated also by several collectors), jack apple (Shafer 559). – **Guadeloupe:** barbacoa (QUESTEL 1951, FOURNET 1978), barbacoar (DUSS 1897, FOURNET 1978, SASTRE & BREUIL 2007), barbakwa (FOURNET 2002), barbaquois (LITTLE et al. 1974), bois noire (LITTLE et al. 1974), bois-négresse (DUSS 1897, LITTLE et al. 1974, FOURNET 1978, SASTRE & BREUIL 2007), bwa néggrès (FOURNET 2002). – **Dominica:** babara [sometimes spelled also "barbara"] (HODGE & TAYLOR 1957, HOWARD 1961, LITTLE et al. 1974, NICOLSON 1991, indicated also by several collectors), babawa [Creole-Patois] (Stijfhoorn et al. 848, Hodge & Hodge 3282), bambarat (LITTLE et al. 1974, NICOLSON 1991), black apple (HODGE & TAYLOR 1957, LITTLE et al. 1974, NICOLSON 1991), bois bambarra (IMRAY et al. 1909), bois noué [bois noir] (Jérémie 1211). – **St. Lucia:** barbara (Barrier 4435). – The name zapote negro was sometimes misapplied by confusion to this species, but it applies to *D. nigra* (= *D. digyna*) only.

Use: According to HODGE & TAYLOR (1957), "the fruits of babará (or sometimes chipped pieces of the bark) are crushed and placed in sacks or baskets which are then immersed in river-pools to drug the fish. The latter are stupefied and rise to the surface where they float bottom up as if dead. Fish so caught are, however, perfectly edible. Unlike another fish-drug, nivrage (...), babará must be removed from the pool after use as its properties are not exhausted quickly" – The pounded seeds (DUSS 1897, FOURNET 2002) and roots (HOWARD 1989, FOURNET 2002) are also used as a fish poison. Several other authors mentioned also the piscicidal properties, e.g., IMRAY et al. (1909), URBAN (1910, as

"*D. ebenaster*"), GRESHOFF (1913: 129, no. 143), SCOTT (1915), HOWARD (1961, 1989), LITTLE et al. (1974), ACEVEDO-RODRÍGUEZ (1990), and NICOLSON (1991).

The wood is dark gray and hardly putrescible (FOURNET 2002) and was used in carpentry and for constructions on the water or for such which are in contact with humid soil (DUSS 1897, QUESTEL 1951). The tough and strong wood was employed for oars, mortar pestles, and for inside house work (IMRAY et al. 1909). The ripe fruits are sometimes eaten (HOWARD 1989, FOURNET 2002). Due to the confusion between *D. nigra* (= *D. digyna*) and *D. revoluta* (see above), this could, however, apply in reality to the former only which is or was often cultivated for its edible fruits. According to IMRAY et al. (1909), and LITTLE et al. (1974), the fruits are, however, poisonous, but this could apply only to the unripe ones. It is sometimes cultivated as an ornamental tree, e.g., in Taiwan (LU et al. 2010).

Specimens examined: **Haiti**, Nord-Ouest, Massif du Nord, Port de Paix, Haut-Piton, 1000 m, [19°52' N, 72°45' W], high limestone ridge, (st), 8–10 Aug. 1925, **E.L. Ekman 4595** [EHH n.s., G ex S, K, LL], "arbor mediocrio"

USA, Puerto Rico, Maricao, Bo. [Barrio] Maricao Afuera, Maricao Forest Reserve, Río Maricao margins, 500 m, 18°09'43" N, 66°59'15" W, serpentine soil, (fr), 10 Jan. 1995, **J.A. Cedeno & P. Acevedo-Rodriguez 388** [MAPR n.s. (dig. photo)], "dark bark; fruits green, rounded"; – same area: along Maricao River, between 0.5 & 1 km up river from entrance to fish hatchery, 485–545 m, 18°10.191' N, 66°59.163' W, riparian vegetation, moist forest, (fr), 10 Jan. 1995, **P. Acevedo & J.A. Cedeno 7177** [US], "tree 15 m tall; trunk ca. 25 cm diam.; bark blackish; fruit nearly globose, green"; – same area: [ca. 18°9' N, 67°1' W], (fr), Apr. 1933, **G.A. Gerhart s.n.** [NY], "tree 20 m"; – Arecibo, Bo. [Barrio] Sabana Hoyos, Finca Las Abras, ca. 340 m, ca. 18°20'14" N, 66°36'15" W, on mogote slope, (st), 14 Sep. 2002, **J.C. Trejo-Torres, J. Miguel Santiago & R. Rodríguez 1778** [UPRRP n.s. (dig. photo)], "tree 3 m; leaves dark shiny green blade and yellow central vein above, light green beneath"; – La Sardinera, [ca. 18°28' N, 66°17' W], coastal forest, (fr), 27 Jan. 1925, **N.L. Britton, E.G. Britton & K.R. Boynton 8155** [NY (+ carp.), S, US]; – same tree: (fl female), 27 Jan. 1926, **N.L. Britton 8508** [GH n.s., NY, S, US]; – prope Toa Alta, [18°23' N, 66°15' W], in sylvis, (fl male), Jun. 1888, **A. Stahl 872** [FHO (fragm.), GH, S 4×, SI, US 2× n.s. (dig. photos), Z 2×].

Montserrat, St. Georges, North Centre Hills, 300 m, [16°46' N, 62°11' W], secondary forest, (fr), 13 Nov. 1945, **J.S. Beard 432** [K], "tree 12 m, 30 cm dbh; bark black as though charred; fruit spherical, 2" diam." – St. Peter, above Salem, [16°45' N, 62°13' W], woods, (fl male), 5–14 Jan. 1961, **R.A. Howard & E.S. Howard 15104** [A, BM, BR, FHO (fragm.), U], "tree 40' tall, dbh 12"; bark black; inner bark with orange juice; staminate fls. in clusters of 3; calyx square, lobes blunt, thick"; – same data, (fl female, fr), **15117** [A, BM, BR, FHO (fragm.), U], "tree 30' tall, dbh 12"; bark black; branches erect, nearly fastigiate; flowers mostly borne singly; calyx strongly 4-angled; corolla yellowish-fleshy, glabrous; pistil globose, pubescent; fruit 5 cm diam. mature"; – same area: 500–1000 ft., (fr), 26 Jan. 1959, **G.R. Proctor 18897** [A, BM, FHO (fragm.), US], "small tree; fruits green; 4–8-seeded"; – same area: roadside, (fr), 16 Feb. 1907, **J.A. Shafer 559** [F, NY, US n.s.], "tree 40 ft."; – Olveston area, Central Hills, [16°44' N, 62°13' W], (fr), 19 Mar.–16 Apr. 1979, **R.A. Howard, E.S. Howard & P.G. Howard 18980** [A, AAU, BM, G, JBSD n.s. (dig. photo), NY], "tree 60' tall, dbh 24"; trunk and branches black; young fruit green, old fruit black" – without further data, [ca. 16°44' N, 62°12' W], upper regions of woodlands, (fr), 21 Feb. 1980, **R.A. Howard & E.S. Howard 19675** [A, NY], "tree 11 m, 30 cm dbh; fruit purple when mature"

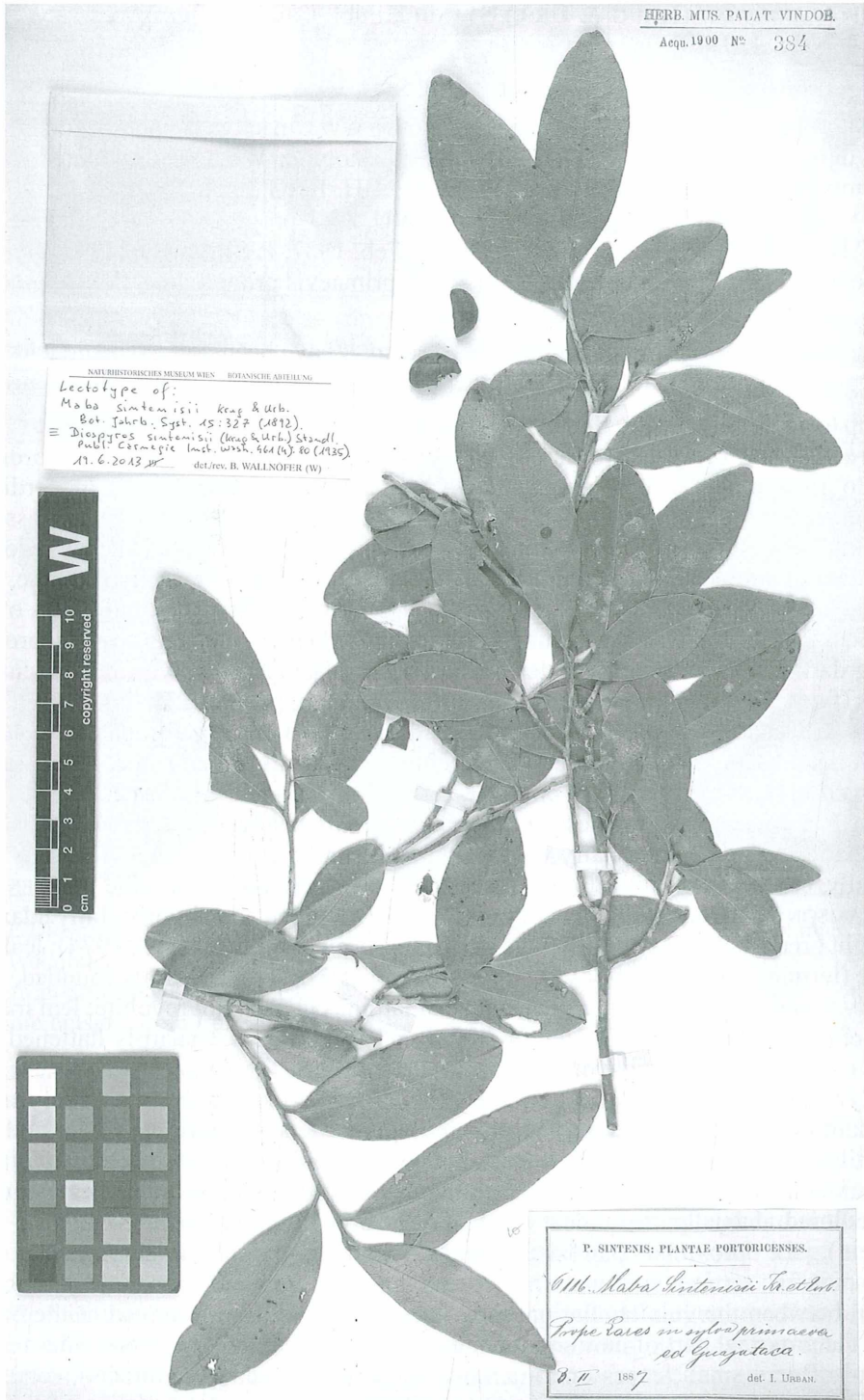
Guadeloupe, Massif de Houelmont, [15°59' N, 61°42' W], (fl male, fr), 1893, **A. Duss 2573** [NY (+ carp.), Z 2×], "arbre d'assez grande taille; écorce noire fortement fendillée; bois très dur, jaunâtre très amère; fleurs blanches, o odeur forte et agréable; assez rare"; – dans les bois de Gourbeyre (morne Gobelin) et de Houelmont, [15°59' N, 61°41' W], (fl, fr), 10 Jul. 1893, **A. Duss 957** [P], "grand arbre à écorce très fendillée et noire"; – Basse-Terre, Mts. Caraïbes, Morne Grande Voute, 500 m, [15°58' N, 61°41' W], (fr), 25 Apr. 1974, **C. Sastre, F. Sastre & J. Fournet 2703** [A n.s., GUAD n.s., P], "arbre 15–20 m; écorce rugueuse noire, bois jaune; fruits verts à calice persistant noir"; – Pointe Montagne, [16°1' N, 61°37' W], (st), 2 Mar. 1939, **A. Questel 4082** [US]; – Marie Galante, vicinity of Pointe de Folle

Anse, 1–2 m, [15°56' N, 61°19' W], coastal forest, (st), 5 Dec. 1959, **G.R. Proctor 20290** [A], "small tree, sterile"; – same data: (fl male), 27 May 1960, **21068** [A, BM, MICH, US], "tree 20 m tall, dbh 6 dm; bark dark brown, scaly; flowers cream, very fragrant"; – same area and coordinates: "régénérations", (st), 5 Apr. 1982, **S. Barrier 5441A** [P], "grand arbre 18 m, 100 cm diam., assez commun"; – (flbuds), 5 Oct. 1981, **S. Barrier 3215** [GUAD n.s., P], "arbre 10 m, 100 cm diam.; écorce noire; nervures des feuilles transparentes"; – without further data, (fl male), 1944–1946, **P. Béna 321** [P]; – in sylvis udis, (st), s.d., **E.P. Duchassaing s.n.** [P 2×].

Dominica, **St. John**, Capucin, [15°38' N, 61°28' W], (fl female), 18 Jul. 1983, **J. Jérémie 1211** [P n.s. (dig. photo)], "arbre ca. 8–10 m; feuilles vertes, brillantes, plus claires dessous; fleurs femelles jaunâtres"; – same locality: (fl female), 18 Jul. 1983, **A. Assi et al. 16424** [GUAD n.s., P n.s. (dig. photo), US n.s.]; – Pointe Ronde, [15°33' N, 61°29' W], (fl female), 29 Jun. 1982, **S. Barrier 3613** [P 2×], "arbre 14 m, 40 cm diam.; écorce noire; bois jaune; fruit globuleux 4/5 cm diam."; – same locality: formation secondaire, (fr), 29 Jun. 1982, **S. Barrier 3623** [P], "arbre 12 m, 40 cm diam.; fruit sec D. [diam.] 4 cm"; – midway along road between Pointe Ronde and Milton Estate, ca. 350 m, [15°33' N, 61°29' W], transitional forests (between xerophytic and mesophytic zones), (fr), 10 Apr. 1940, **W.H. Hodge & B.T. Hodge 2676** [GH, US], "tree 25 ft., 6" diam.; bark black; fruit 1" diam.; common" – **St. Andrew**, Hampstead, [15°36' N, 61°23' W], (fl male), 1903, **F.E. Lloyd 662** [NY]; – Bense, [15°35' N, 61°22' W], (fl male), 3 Jul. 1982, **S. Barrier 3692** [P 2×], "arbre 8 m; fleur crème, parfumée de type 4, légèrement asymétrique; calice carré, corolle très charnue 16 étamines"; – slopes between coastal road and bay E of Pointe Baptiste, ca. 30 ft., [15°36' N, 61°21' W], (fl male), 4 Jul. 1965, **W.R. Ernst 1831** [BM, US], "small tree; corolla white"; – 1 mile N Calibishie, [15°36' N, 61°21' W], scrubby, windswept coastal vegetation along road, (fl male), 23 Apr. 1940, **W.H. Hodge & B.T. Hodge 3177** [GH, US], "tree 8 m, 20 cm diam.; bark dark; petals of flowers withered but look as though they were yellow-green"; – Woodford Hill, 30 m, [15°34' N, 61°20' W], roadside, (fl male), 12 Jun. 1977, **D.H. Nicolson 4239** [US], "common tree with dark bark; flowers 4-merous, greenish, staminate"; – Deux Branches, 700 ft., [15°29' N, 61°18' W], (st), 2 Dec. 1964, **D.H. Nicolson 2132** [US], "tree to 50 ft.; wood yellow; bark black" – **St. David**, along Carib trail from Salybia [= Salibia] to Concorde Valley (Roseau Track), Carib Reserve, [15°29' N, 61°16' W], common throughout dry woodlands, (st), 1 May 1940, **W.H. Hodge & B.T. Hodge 3282** [GH], "bark dark"; – Madjini, 30 m, [15°28' N, 61°16' W], (fr), 1 Feb. 1969, **D.H. Nicolson 4136** [US], "trunk dark, scaly; calyx persistent 4-merous; petals white, united at base, 4–6-merous; carpel 8-seeded"; – Roche Marqué, hillsides above Rosalie Point, 25–100 ft., [15°22' N, 61°17' W], mesophytic woodland, (fl male), 22 Jun. 1965, **G.L. Webster 13473** [CAS, DAV, US n.s.], "tree 15 m high; flowers white, pendent"; – S of Rosalie ca. 1.5 miles along road to La Plaine, ca. 500 ft., [15°21' N, 61°16' W], woodland, (fl male), 18 May 1964, **W.R. Ernst 1364** [BM, GH, US], "tree ca. 8 m; wood yellowish from sap; flowers square; corolla white" – **St. George**, Trois Pitons, [15°22' N, 61°20' W], (fl male), 1903, **F.E. Lloyd 763** [NY]; – vicinity of Laudat, [15°20' N, 61°20' W], (fr), 13 Mar. 1940, **W.H. Hodge 2091** [GH], "fruits grow 3× size of this specimen"; – ridge N of Roseau valley, [15°19' N, 61°23' W], cultivated, (fr), Mar.–Apr. 1996, **C. Whiteford 7271** [BM, MO n.s.], "slender tree, about 12 ft. tall; black wood [? bark]; glossy fruit" – **St. Patrick**, La Plaine windward, [15°20' N, 61°15' W], (st), 10 Jan. 1889, **G.A. Ramage s.n.** [K 2×]; – 200 m up from beach along Ravine Daroux, Petite Savane, 15 m, 15°14' N, 61°16' W, secondary rainforest, (fl female), 10 Jun. 1992, **E. Stijfhoorn, G.A. Eidsen, L. Moise & H.T. Beck 848** [GH n.s., NY], "tree 8 m × 12 cm; wood white, hard; bark black, non-fibrous; leaves with shiny yellow midvein, identic tip; resin slight, clear" – without further data, (fr), 8 Jun. 1888, **H.A.A. Nicholls s.n.** [K], "high forest tree"; – (fr), 24 Feb. 1892, **H.A.A. Nicholls s.n.** [K]; – (fr), Jan. 1971, **J. Archbold s.n.** [US], "fruit green when collected"; – Botanic Gardens, (fl female), 26 Nov. 1914, **J. Jones 2956** [K].

St. Lucia, **Dauphin**, Louvet estate, 600 m, [13°58' N, 60°52' W], forêt mésophile, (fl male), 12 Oct. 1983, **S. Barrier 4435** [P, U], "petit arbre, 10 m; abondant; fleurs et fruits" – **Dennerly**, Mount La Combe, 50 m south of summit, ca. 450 m, [13°54' N, 60°57' W], exposed, well-drained ridgetop with low tree canopy, (fl female), 5 Aug. 2005, **R. Graveson & M. Smith 1137** [UPRRP n.s. (dig. photo)], "tree 8 m; petals yellow"; – Barre de l'isle trail to Mt. La Comb [= Mount La Combe], [13°54' N, 60°57' W], (fr), 24 Jan. 1985, **R.A. Howard, E.A. Kellogg, V. Slane, P.F. Stevens & L. Jean-Pierre 19858** [A, BM, NY], "shrub with erect branches, to 5 m tall; bark black, inner bark yellow; fruits green"; – **Vieux-Fort**, Moule à Chique, [13°43' N, 60°57' W], (defl male, yfr), 17 Nov. 1982, **J. Fournet H-3874** [GUAD n.s., P n.s. (dig. photo)], "arbre 4–5 m"

Antilles, in magnis sylvis Tortosae [not traced], (fl), s.d., **L.C. Richard s.n.** [P].

Fig. 9: Lectotype of *Diospyros sintenisii* (KRUG & URB.) STANDL. [W].

Diospyros sintenisii (KRUG & URB.) STANDL., Publ. Carnegie Inst. Wash. 461 (4): 80 (1935), – [fig. 4, 9–10].

≡ *Maba sintenisii* KRUG & URB., Bot. Jahrb. Syst. 15: 327 (1892).

Typus: prope Lares ed Guajataca, [18°22' N, 66°55' W], in sylva primaeva, (defl female, seeds only), 3 Feb. 1887, **P. Sintenis 6116** [Lectotype: W (here designated, fig. 9), isolectotypes: B (destroyed), BM, F 3×, G 4×, GH, HBG 2×, K 2×, L 2×, LE 2×, M, MO 3×, NY 2×, P 3× (+ carp.), S, US 2×, W, WU, Z]; – prope Lares, ad Callejones, [ca. 18°17' N, 66°52' W], sylvis primaevae, (st), 12 Feb. 1887, **P. Sintenis 6227** [syntypes: B (destroyed), E, GOET]; – in fruticetis et sylvis primaevae prope Lares, **P. Sintenis 6042** [syntype: B (destroyed), duplicates not traced].

Note: The seeds being part of Sintenis 6116 seem to have been collected and added at a later point. The corresponding carpological collection at P bears the date "1er Juin 1889"

Tree up to 15 m tall (already flowering when 6 m tall), with a trunk diameter up to 15 cm, evergreen; wood brown, hard, heavy and strong; bark dark gray (brown according to Cedeno 191), smoothish, becoming slightly fissured with short cracks (according to Breckon et al. 7872: "flaky in small scales"); inner bark thin, light pink, tasteless (data on trunk diameter, wood and bark according to LITTLE et al. 1974); **indumentum** consisting of simple, appressed or slightly spreading, straight or slightly flexuose, light-colored hairs of different length; young twig apices densely hairy; young twigs often ± flattened, later on subterete, medium densely hairy when very young, soon glabrescent, drying dark brownish to gray; older twigs gray or blackish-gray, with raised lenticels; **leaves** (fig. 10a) alternate, with brochidodrome venation; petioles 2.5–4 mm long, 1–1.5 mm thick, ± canaliculate adaxially, light brown, scattered hairy, glabrous when old; leaf lamina lanceolate or less frequently ± elliptic, very rarely obovate, sometimes ± asymmetric, (1.5–) 5–12 (–16.5) cm long, (1–) 2.5–5.8 cm wide, (1.3–) 2–3 (–3.8) times longer than wide, usually widest in the middle, firmly chartaceous, glabrous adaxially, soon glabrescent (scattered hairy when young) abaxially, gray-brown and slightly shiny adaxially, characteristically fuscous (dark grayish-brown; see color table in BEENTJE & WILLIAMSON 2010) and dull abaxially when dry, dark green and slightly shiny adaxially, and light green and dull abaxially when alive (according to LITTLE et al. 1974); leaf apex obtuse (terminal apex retuse or very rarely mucronate) or less frequently rounded, rarely broadly rounded, acute or emarginate; base of lamina cuneate, not revolute; leaf margins ± entire (minutely irregular), ± flat or slightly revolute, with a ± sharply flattened, light (cream-colored), well visible marginal vein; flachnectaria few (missing on some leaves), usually present on the proximal ½ of the abaxial leaf surface; midvein ± deeply sunken and glabrous adaxially, markedly prominent and scattered hairy (glabrescent with age) abaxially, frequently light-colored on both sides (according to LITTLE et al. 1974: light yellow when alive); secondary veins ca. 7–8 per side, prominent on both sides, frequently light-colored abaxially, those near the leaf-apex obtuse-angled (± perpendicular to the midvein), the proximal pair acute-angled and ± straight; intersecondary veins inconspicuous; tertiary and quaternary veins raised on both sides, markedly reticulate; area in-between the veinlets flat on both sides; **inflorescences** arranged at the base or along the proximal part of new shoots in the axil of leaves (the lowermost ones often in the axil of very small leaves or sometimes in the axil of caducous bracts), sometimes slightly concaulescent; male inflorescence units up to 1 cm long, consisting of a simple, (1–) 2–3-flowered cyme (fig. 10b); peduncles 2–3 mm long, 0.8 mm thick, densely hairy;

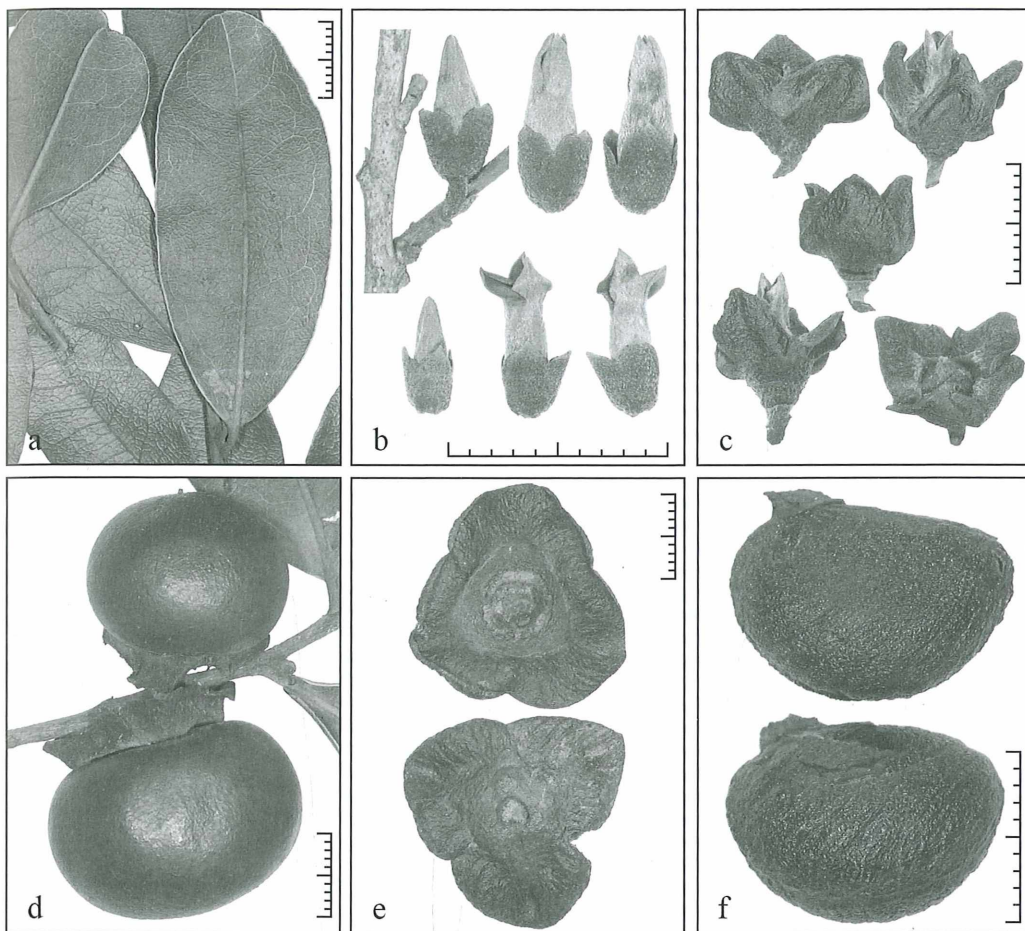


Fig. 10: *Diospyros sintenisii*: a: leaf surfaces (from Otero & Gregory 971 [A]); – b: male flowers (from Woodbury 18.11.1966 [BRIT]); – c: female flowers (from Otero & Gregory 971 [A]); – d: fruits (from Stimson 3462 [DUKE]); – e: calyces of fruits (on top: as seen from inside, bottom: as seen from outside; from Little 13321 [BM]); – f: seeds (from Otero & Gregory 971 [A]); – scale = 1 cm.

pedicels 0.5–1 mm long, ca. 0.8 mm thick, densely hairy; female cymes 1-flowered; stalk (peduncle and pedicel) 2–3 mm long and in the middle 1.5 mm thick, with same sort of hairs as on male flowers; bracteoles of male and female flowers 2–3.5 mm long and 1–1.5 mm wide, acute or obtuse, medium densely hairy abaxially, glabrous adaxially, soon caducous; **flowers** 3 (–4)-merous; male flowers (fig. 10b) 11 mm long (pedicels excluded) at anthesis [Woodbury s.n.]; calyx 4–4.5 mm long and ca. 2.5 mm wide, undivided in the proximal 3–3.5 mm, without longitudinal ridges, medium densely covered with short, appressed hairs on the outside, glabrous inside, green when alive; calyx lobes \pm 1 mm long, 2–2.5 mm wide, \pm triangular, \pm acute; margins of lobes flat; sinuses between the lobes inconspicuous; corolla ca. 9 mm long, cream when alive (Acevedo-Rodríguez & China 11657), densely covered with long, appressed, straight,

light hairs, glabrous inside; tube ca. 8 mm long, widest in the middle and there 3 mm wide; throat narrow (ca. 1 mm wide); corolla lobes broadly ovate, ca. 4.5 mm long and 1.5–2 mm wide, acute, glabrous adaxially; stamens 12 (only one flower bud of Woodbury s.n., 18 Nov. 1966, dissected), strongly differing in length, 1.5–4 mm long, usually in pairs (the outer long and the inner one short), glabrous (except one stamen with a hairy filament and connective adaxially), adnate to the corolla tube near its base; filaments 0.5–2 mm long and ca. 0.2 mm wide, flat; anthers 1.2–2.2 mm long and ca. 0.5 mm wide, widest in the proximal third, the outer cuneate and the inner ones truncate proximally, tapering into a conical connective appendage distally; rudiment of the ovary consisting of an irregular, densely hairy lump of tissue, lacking stylodia; **female flowers** (Otero & Gregory 971, fig. 10c) 10 mm long (pedicels excluded); calyx ca. 10 mm long and ca. 12 mm wide, undivided in the proximal 4–5 mm, on the outside medium densely covered with short, ± appressed hairs (but scattered hairy or glabrous towards the apex and margins of lobes), on the inside scattered hairy on distal and densely hairy on the proximal parts, without a longitudinal ridge running down from the sinuses abaxially; calyx lobes 7 mm long, 7–9 mm wide, broadly triangular, ± obtuse, with slightly involute (flexed towards the inside) or flat margins near base; proximal half of the lobes adaxially with a gable-like, raised, densely hairy step (fig. 10c: right side on bottom, 10e: on top); area around the sinuses between the calyx lobes expanded and protruding outwards; corolla ca. 9 mm long, color not known, not exceeding the calyx lobes, densely covered (except at base) with long, appressed, straight, light hairs on the outside, glabrous inside; tube ca. 5.5 mm long and ca. 4 mm wide, widest in the distal third, on proximal half not cylindrical (deformed due to the internal shape of the calyx); throat ca. 1.5 mm wide; corolla lobes ca. 4 mm long and 3.5–4 mm wide, ovate, ± acute, glabrous adaxially, on abaxial side densely hairy along the keel, scattered hairy towards the margins and there glabrous; staminodia 3 (only one anthetic flower dissected), antesealous, 1.6–2 mm long, flat, glabrous, sunken in narrow, deep, longitudinal cavities at the base of the ovary (therefore hardly visible), adnate at the base of the ovary (or corolla tube); filaments ca. 0.8 mm long and ca. 0.4 mm wide; antherodes flat, triangular, ca. 1 mm long and 0.6–0.8 mm wide at base; ovary 6-locular, as a whole 5 mm long, 2.5 mm in diameter in the proximal third, tapering into the ca. 1.5 mm long, conical style, medium densely covered with appressed, ± straight, light hairs; stylodia 3, fused together up to the apex; stalk of the **fruits** up to 1.5 mm long, 2–3 mm thick, covered with remnants of the indumentum; fruits (fig. 10d) up to 6-seeded, depressed globose, 2.5–3 cm in diameter, shiny green and later orange-yellow (Cedeño 191) when immature, becoming brown or dark red when alive and ripe (LITTLE et al. 1974, Little 13321), fuscous, slightly shiny and with tightly adhering epidermis when dry, distally with the mucro-like remnant of the style, detaching with the calyx, smooth or with a slightly granulate surface (with subepidermal stone cell granules) when dry; maturing fruits glabrous except at the apex; fruit wall with a stone cell layer, 1 mm thick when dry (according to LITTLE et al. 1974: hard-walled when ripe); calyx as a whole up to 2.5–2.8 cm wide and 0.5–0.8 cm high (fig. 10e), green when alive, obtusely triangular, with a granulate surface (subepidermal stone cell granules), glabrescent on the outside, on the inside with some remnants of the indumentum on the exposed (uncovered) parts and densely covered with appressed, long hairs on the proximal parts appressed to the fruit; area around and below the sinuses between the calyx lobes expanded and protruding step-like out- and downwards; undivided (basal) part of the calyx 0.9 cm wide, without longitudinal ridges running down from the sinuses

abaxially; lobes 1.6–1.8 cm long and 1 cm wide, involute basally; seeds (fig. 10f) formed like the segments of an orange or sometimes coffee-bean shaped, 1.5–1.8 cm long, 1–1.2 cm wide, 0.8–1 cm thick, brownish when dry (blackish according to LITTLE et al. 1974); outer tangential (periclinal) wall of the exotestal cells finely striate below the surface; endosperm ruminant (seed-surface with some transversal, bent lines or furrows).

Figure: branch with female flowers, fruits and leaves (LITTLE et al. 1974: fig. 649; same plate reproduced in LIOGIER 1995: fig. 113-1).

Distribution, habitat and phenology: It is known only from Puerto Rico, (fig. 4). According to LITTLE et al. 1974, it is "uncommon in moist limestone and lower cordillera forests at 300–2500 feet [90–760 m] altitude in mountains of western Puerto Rico" and was "collected as far east as Bayamón and west to Susúa and Maricao" AXELROD (2011) stated: "Tree in northern limestone hills, Río Abajo Forest Reserve, Susúa Forest Reserve, Maricao Forest Reserve; 50–800 m" Collectors reported it from moist, sometimes disturbed forests (but Little 13321 is from a dry forest) on limestone hills (which are often called mogotes). Breckon et al. 7872 reported it from an "evergreen, sclerophyllous forest on serpentine in mesic canyon with permanent stream in bottom" and Cedeño 191 found it on "serpentinic soil" It was indicated from elevations at ca. 60–1160 meters and was collected in flower in June, August and November, and in fruit in March, and from June to November. LITTLE et al. (1974) reported it to be flowering in spring and fruiting in summer, and AXELROD (2011) indicated it to be in flower from April to June and in fruit from October to July.

Vernacular names: guayabota níspero, guayabota, tabeiba, múcaro (LITTLE et al. 1974, LIOGIER 1995, AXELROD 2011; – at least some of these names are also indicated by URBAN 1892, 1910, BRITTON & WILSON 1925, OTERO et al. 1945 and ACEVEDO-RODRÍGUEZ & STRONG 2012). On herbarium labels it is called tabeiba by Vélez 1587 and múcaro by Little 13321.

Specimens examined: **USA, Puerto Rico**, Quebradillas, Bo. [Barrio] Cocos, mogotes (limestone hills) E of Rt 482 & N of Rt 483, east-central mogote, N slope, ca. 130 m, 18°28.99' N, 66°54.68' W, disturbed forest in limestone hills; growing at the base of a small cliff, (st), 14 Sep. 2005, **F. Axelrod, A. Cubiñá & C. Laboy 13139** [UPRRP n.s. (dig. photo)], "tree 2–3 m"; – Tree-Quebradillas area (P. Vives), [18°28' N, 66°56' W], (st), May 1987, **Bro. (Brother) Alain (= E.E. Liogier) 36343** [NY]; – Maricao, Bo. [Barrio] Maricao Afuera, Maricao Forest Reserve, Río Maricao drainage, shaded humid, NW facing slope of branch ca. 1 km from fish hatchery, 630 m, 18°9'43" N, 66°59'28" W, (fr), 9 Oct. 1993, serpentinic soil, **J.A. Cedeño 191** [MAPR n.s., NY n.s. (dig. photo)], "tree 8 m, 12 cm DBH; bark brown; fruits rounded, orange-yellow"; – Distrito de Aguadilla, Mun. de Maricao, Maricao Insular Forest Reserve, ca. 3800 ft., [ca. 18°9' N, 67°1' W], forest north slope below the campamento, (fr), 13 Jul. 1966, **W.R. Stimson 3462** [DUKE, GH n.s., LL, MICH, MO, UC, US n.s. (dig. photo)], "tree; fruit green"; – same area and coordinates: (st), 1933, **G.A. Gerhart s.n.** [NY]; – (fl female, fr), 8 Aug. 1944, **J.I. Otero & L.E. Gregory 971** [A 2×]; – (fr), s.d., **L.R. Holdridge 23** [NY], "25 ft."; – Municipio de Yauco, Barrio Susúa Alta, bosque estatal de Susúa, ca. 700–800 m del cruce, en las márgenes de Quebrada Peces, lado sur de la carretera que va a la oficina, 150 m, 18°4'30" N, 66°55'30" W, vegetación con *Clusia rosea*, *Gesneria pedunculosa*, *Neolaugeria resinosa* y *Tabebuia haemantha*, (fr), 7 Sep. 1990, **R. García & G. Caminero 3159** [JBSD n.s. (dig. photo), MAPR n.s.], "árbol 7 m; cáliz y fruto verde"; – Susúa Forest Reserve, Quebrada Peces between road to Campamento Susúa and washed-out bridge on dirt road, 120–130 m, 18°04'08.8" N, 66°54'35.5" W, evergreen, sclerophyllous forest on serpentine in mesic canyon with permanent stream in bottom, (fr), 24 Jul. 2006, **G.J. Breckon, I. Morales, J. Cancel & J. Metcalf 7872** [MAPR n.s. (dig. photo)], "tree, dbh 10 cm; bark dark grey, flaky in small scales; fruits green"; – same area: 1800 ft., [18°2' N, 66°54' W], dry forest, (fr), 10 Jul. 1950, **E.L. Little, jr. 13321** [BM, GH, NY], "tree 20 ft. high, dbh 3 in.; fruits green (immature) turning dark red"; – Arecibo, 5 km S of Biáfara, ca. 60 m, 18°24' N, 66°39'53" W, karst limestone hills; remnant moist forest, (fr), 25 Jun. 2001,

P. Acevedo-Rodríguez & D. Chinea 11649 [NY n.s. (dig. photo), UPRRP n.s. (dig. photo), US n.s. (dig. photo)], "tree 8 m with gray bark; fruits depressed-globose, green"; – same data, (fl male), **11657** [NY n.s. (dig. photo), UPRRP n.s. (dig. photo), US n.s. (dig. photo)], "tree 6 m; calyx green; corolla cream"; – 5 miles SE of Arecibo, 800 ft., [18°25' N, 66°40' W], moist limestone forest, (fr), 3 Jul. 1966, **E.L. Little, jr. 21595** [BM, F, GH, NY, US], "tree 50 ft. high, dbh 4 in.; bark dark gray, smoothish, becoming slightly fissured, with short cracks"; – Miraflores, NW of Florida, Rd. 637, [18°25' N, 66°39' W], (fl male), 18 Nov. 1966, **R.O. Woodbury s.n.** [BRIT, MO]; – Utuado, Río Abajo Forest Reserve, S of road 621, fourth mogote if coming from the reserve office, [ca. 18°20' N, 66°41' W], medium forest on mogote W slope, (st), Jun. 1999, **J.C. Trejo-Torres & A. Alicea 1388** [UPRRP n.s. (dig. photo)], "tree, not common; leaf shape irregular in some individuals"; – Arecibo, Bo. [Barrio] Río Arriba, sinkhole ca. 1 km from S end of pilot road for proposed Rt 10, ca. 250 m, 18°20.33' N, 66°40.67' W, forest in limestone hills, (fr), 8 Mar. 1995, **F. Axelrod 8827** [NY], "tree ca. 6 m; fruit green, globose"; – Arecibo, Bo. [Barrio] Sabana Hoyos, Finca Las Abras, ca. 410 m, ca. 18°20'15" N, 66°36'13" W, on mogote top, (st), 16 Oct. 2002, **J.C. Trejo-Torres 2009** [UPRRP n.s. (dig. photo)], "4 m"; – Toa Alta, [18°23' N, 66°15' W], (fr), 6 Nov. 1965, **R. Woodbury s.n.** [BRIT, F, NY]; – Sabana seca, [ca. 18°26' N, 66°12' W], (st), 1 Mar. 1959, **R. Woodbury s.n.** [NY, US]; – Serpentine hills [not traced], (defl female), 19 Apr. 1941, **J. Vélez 1587** [BRIT]; – Monte del Estado [not traced], (fl male), Jun. 1970, **R.O. Woodbury s.n.** [NY 2×], "tree 5" × 30"

Acknowledgements

I wish to thank Walter Till (WU) for critically reading the manuscript, Ines M. Ternbach (Vienna) for correcting the English, Heimo Rainer (Vienna) for allowing me to use his ArcMap 10 application for creating the distribution maps, our librarians Andrea Kourgli and Gabriele Palfinger (both: Vienna), Pedro Acevedo-Rodríguez (US), Mark Strong (US), Franklin S. Axelrod (UPRRP), and Francisco Jiménez (JBSD) for procuring rare literature and / or digital images of specimens. Last but not least, I am grateful to the directors and curators of ca. 80 herbaria who kindly made their herbarium material available.

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Zeitschrift/Journal: [Annalen des Naturhistorischen Museums in Wien](#)

Jahr/Year: 2014

Band/Volume: [116B](#)

Autor(en)/Author(s): Wallnöfer Bruno

Artikel/Article: [A revision of neotropical Diospyros \(Ebenaceae\): part 7 153-179](#)