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A revision of neotropical *Diospyros* (Ebenaceae): part 5

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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. 75 herbaria have been studied. The Central and South American, quite variable species *Diospyros juruensis* A.C.Sm. is here described in detail and is divided into the following taxa: subsp. *juruensis* (synonym: *D. crotalaria* Provance & A.C.Sanders), subsp. *campechiana* (Lundell) B.Walln. (synonym: *D. camposii* Provance & A.C.Sanders), subsp. *hartmanniana* (S.Knapp) B.Walln. (synonym: *D. haberi* Provance & A.C.Sanders), subsp. *nenab* (B.Walln.) B.Walln. and subsp. *panamense* (S.Knapp) B.Walln. A key for identification, figures, distribution maps, and lists of specimens are presented.

Key words: Ebenaceae, *Diospyros juruensis* subsp. *juruensis*, subsp. *campechiana*, subsp. *hartmanniana*, subsp. *nenab*, subsp. *panamense*, *D. campechiana*, *D. camposii*, *D. crotalaria*, *D. haberi*, *D. hartmanniana*, *D. nenab*, *D. panamense*, *D. whitei*, revision, taxonomy, key for identification, distribution maps, flora of Central and South America.

Zusammenfassung

Im Rahmen einer Revision der neuweltlichen Ebenaceae für "Flora Neotropica" und einigen Regionalfloren konnten Herbarbelege aus ca. 75 Herbarien studiert werden. Die mittel- und südamerikanische, sehr variable Art *Diospyros juruensis* A.C.Sm. wird hier im Detail beschrieben und in die folgenden Taxa gegliedert: subsp. *juruensis* (Synonym: *D. crotalaria* Provance & A.C.Sanders), subsp. *campechiana* (Lundell) B.Walln. (Synonym: *D. camposii* Provance & A.C.Sanders), subsp. *hartmanniana* (S.Knapp) B.Walln. (Synonym: *D. haberi* Provance & A.C.Sanders), subsp. *nenab* (B.Walln.) B.Walln. und subsp. *panamense* (S.Knapp) B.Walln. Ein Bestimmungsschlüssel, 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 8 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, 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 (2011); 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; 2× = 2 sheets.

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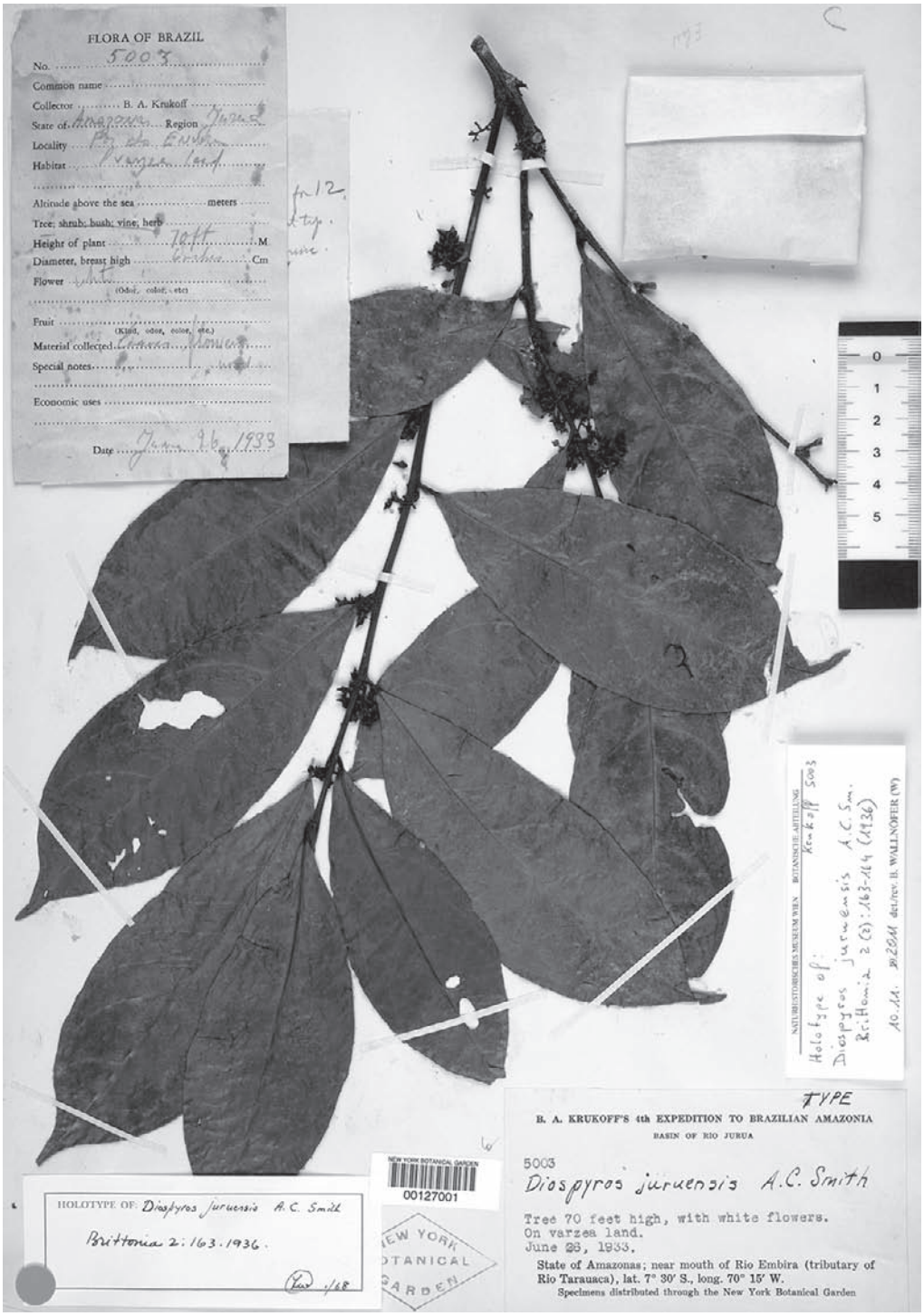


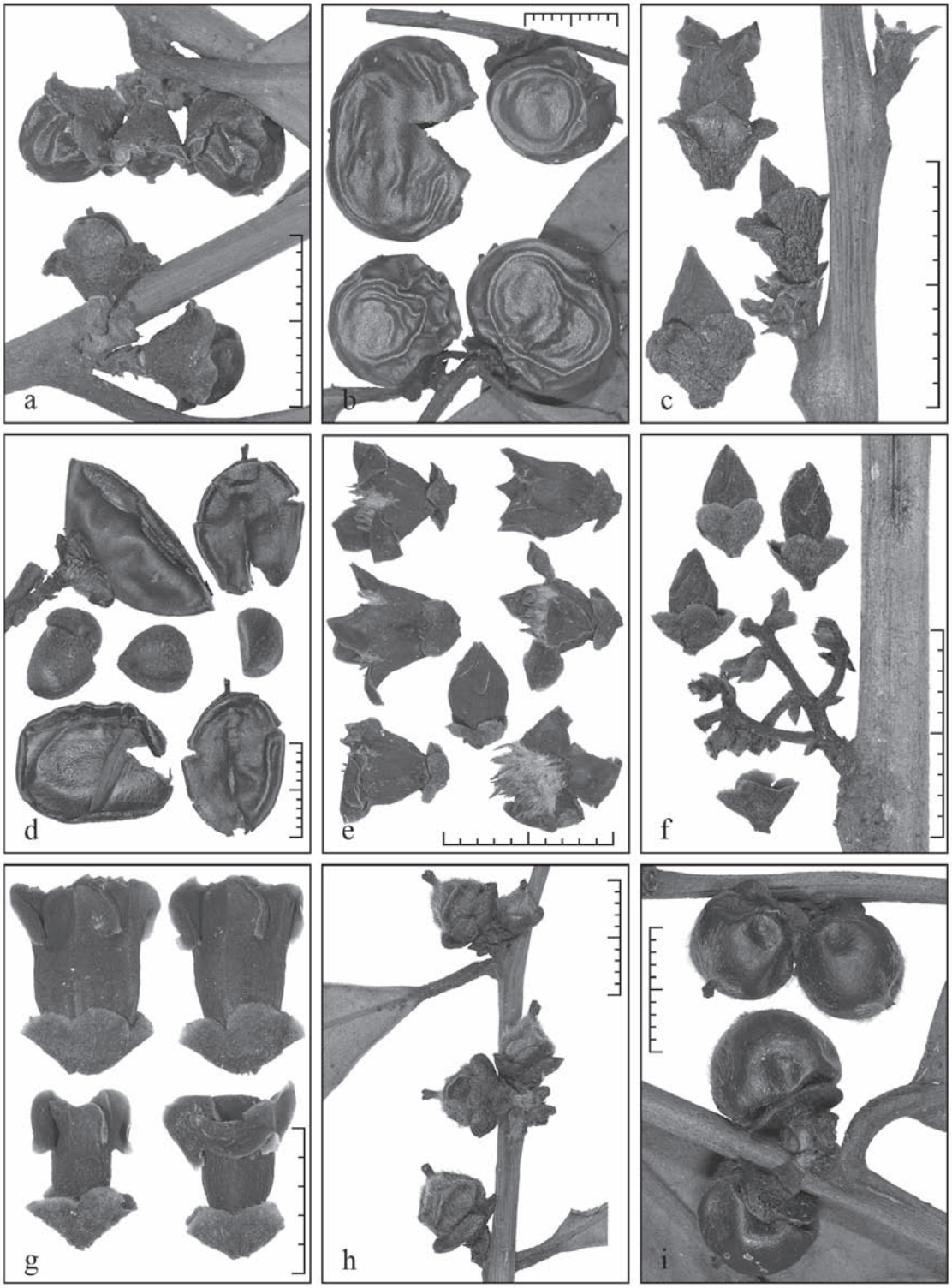
Fig. 1: Holotype of *Diospyros juruensis* A.C.Sm. subsp. *juruensis* [NY].

Diospyros juruensis **A.C.Sm.**, Brittonia 2 (2): 163–164 (1936); sensu lato – [fig. 1–12].

Typus: Brasil, Amazonas, basin of Rio Jurua, near mouth of Rio Embira (tributary of Rio Tarauaca), [ca. 150 m], 7°30' S, 70°15' W, [correct seems to be: 7°20' S, 70°15' W], on varzea land, (fl male), 26 Jun. 1933, **B.A. Krukoff 5003** [holotype: NY, isotypes: A, BM, F (photo F 52500), G, K, LE 2×, M, MICH, MO (Provance & Sanders 2009: fig. 10–11), PR n.s. (dig. photo), RB, S, U, UC, US], "tree 70 ft. high; with white flowers".

The following description applies to the species in a broad sense (sensu lato):

Treelet or tree up to 28 m tall (according to Gilly et al. 343 already flowering when 3 m tall), with dbh up to 50 cm, evergreen; wood soft (Bristan 1229), white and "rank-smelling" (Pitman 726); bark black; inner bark orange (Pitman 726); slash with "foul odor of urine" (Hammel et al. 17100); indumentum (fig. 3a–b, e, 4e) consisting of two-armed (proximal arm extremely short or up to a fourth of length of the distal arm) or sometimes apparently simple (and attached laterally), appressed or slightly spreading, straight or slightly flexuose, light brown, dark brown or black hairs of different length; twig apices, very young leaves and scales of the axillary buds densely hairy; young twigs sometimes hollow or chambered or filled with pith (e.g. in Contreras 4519, Haber et al. 6087), subterete (but often ± flattened and longitudinally ridged below leaf insertions), greenish-gray (like those of *Heisteria*) or gray-brown, often with black patches, soon glabrescent; epidermis of young twigs tightly adhering on some specimens or peeling off on others; young bark (twig apices excluded!) on some specimens bearing also, at least partially, patent, whitish-translucent, simple, stiff, minute hairs (fig. 3c–d; sometimes also present on petioles); older twigs brown to dark brown, smooth (but often with subepidermal, minute granules) on plants from dry habitats or longitudinally wrinkled on those from humid habitats, later on with the longitudinal lenticels widening into shallow fissures; **leaves** alternate, with brochidodrome venation, sometimes partially covered with a ± dense layer of fine crystal needles (probably consisting of naphthoquinones and their derivatives; fig. 4a–b); petioles (3–) 4–18 mm long, 1–2 mm thick, ± canaliculate adaxially, wrinkled, glabrous or scattered hairy; leaf lamina narrowly to broadly lanceolate or ± elliptic, ± oblong in some populations, rarely obovate, usually tapering into the petiole, (1.5–) 5–17 (–27) cm long, (1.5–) 2.5–6 (–9.8) cm wide, (1.2–) 1.7–3.3 (–4.8 in subsp. *nenab*) times longer than wide, chartaceous or less frequently slightly coriaceous, dull and often minutely granulate (especially when young) on both sides (fig. 4c–d), scattered hairy on proximal parts abaxially or completely glabrous; lamina adaxially dark green and ± glossy when alive, darker and dirty gray-brown when dry, abaxially paler green and dull when alive, gray-brown or dark brown when dry (but color depending on drying technique used); leaf apex acuminate (sometimes with a short drip tip), acute, obtuse or rounded; base of lamina usually cuneate, rarely rounded (Bristan 1229) or narrowly truncate (Shrank & Molina 4284 and Folsom 3168, both collected near the Atlantic); leaf margin entire, slightly revolute when dry; flachnectaria minute (fig. 3f), up to ca. 20 (–30) scattered all over the abaxial leaf surfaces but often located near the midvein; adaxial side of midvein glabrous, ± sunken in the proximal half (rarely slightly raised near the base of lamina), slightly sunken or ± flat distally; abaxial side markedly prominent, longitudinally wrinkled, glabrous or especially proximally scattered hairy; secondary veins 5–6 per side, ± flat adaxially, prominent and running down over a few millimeters along the midvein abaxially; intersecondary veins not conspicuous; tertiary and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quaternary veins hardly visible adaxially, flat, rarely slightly raised, often hardly visible abaxially; **inflorescences** arranged along the proximal part (rarely up to the apex) of new shoots in the axil of ± fully developed leaves (the lowermost ones sometimes in the axil of caducous bracts or small leaves), medium densely to densely covered with a brown or black indumentum; male inflorescence units up to 1.5–2 cm long, consisting of a simple, 1–6-flowered cyme (often with additional, small buds and their bracts basally) or few-branched, compact and few-flowered or divaricately branched, expanded and up to ca. 50-flowered (= amplified cymes, often resembling dichasia due to the frequently subopposite position of bracts, fig. 1, 2f; for details see also Wallnöfer 2007: 226 and fig. 8d, Weberling 1981: fig. 113I–II and Provance & Sanders 2009: fig. 10); pedicels 1–2 mm long; female cymes 1–3 (–7)-flowered (fig. 2a–c, h–i, 7, 10–12); stalk (peduncle and pedicel) up to 3 mm long and up to 1 mm thick, near base often with several additional buds and their bracts; pedicels of the lateral flowers ca. 1 mm long; bracts and the often subopposite bracteoles of both sexes similar in shape, 1–2 mm long and 0.6–1.5 mm wide, persisting, broadly triangular or ± ovate, distally rounded or ± acute, sometimes slightly carinate, ± densely hairy abaxially (hairs spreading on margins), glabrous adaxially; **flowers** 4 (–6)-merous; male flowers (4–) 5.5–7 mm long (pedicels excluded), extremely fragrant (Clark et al. 2060, 4631, Pacheco 1981); calyx 1.5–2.5 mm long and (2.5–) 4 mm wide, undivided in the proximal 1–1.5 mm, often with subepidermal, minute, light granules (especially in subsp. *campechiana*), on the outside medium densely hairy, on the inside glabrous in some populations or covered with a dense layer of short and thick, dark hairs in others (fig. 3e); calyx lobes ± semicircular (but sometimes slightly truncate distally), (0.8–) 1–1.5 mm long, 1–2.5 mm wide, imbricate, convex on the outside, very thick in some populations, thinner in others, with spreading hairs on the margins; sinuses between the lobes inconspicuous; corolla (3–) 4–6.5 mm long, greenish or greenish-yellow (or cream) when young, white at anthesis, black when dry, glabrous on both sides (but sometimes on the outside with a few hairs at the base of lobes), often with subepidermal, minute granules; tube 2–3.5 mm long, barrel-shaped, widest in the middle and there 2–3 mm wide; aperture of the corolla 1.5–2 mm wide; corolla lobes ovate, (1.5–) 2–3 mm long and (1.8–) 2–2.5 mm wide, acute or rounded distally, often ± auriculate at base; stamens 16–28 (subsp. *juruensis*: 16 in Krukoff 5003 and Ruiz et al. 2397; subsp. *campechiana*: 16 in Lundell & Contreras 20739 and 18 in Martinez et al. 23380; subsp. *hartmanniana*: 16 in Haber & Bello 7323 and 18 in Haber et al. 5015; subsp. *panamense*: 18 in Clark et al. 2060, 22 in Haber & Cruz 7107, 25 in Espinoza et al. 884 and 28 in Aguilar 2749); stamens (fig. 2, 9, 11, 13 in Provance & Sanders 2009) united in pairs or rarely 3 together (filaments fused together over the whole length or only in their proximal half), ± equal in length (rarely the inner ones shorter), (3–) 4–4.5

Fig. 2: *Diospyros juruensis*: (a) subsp. *juruensis*: young fruits (from Del Carpio et al. 1719 [MO], Peru); – (b) subsp. *hartmanniana*: fruits (from McPherson & Richardson 15959 [MO, isotype], Panama); – (c–d) subsp. *nenab*: (c) female flowers (from Cardenas 2109 [MO], Colombia), (d) young fruits (from Cárdenas 1164 [MO, holotype], Colombia); – (e–i) subsp. *panamense*: (e) male flowers (from Espinoza et al. 884 [W], Costa Rica), (f) inflorescence and male flowers (from Clark 419 [W], Ecuador), (g) male flowers (from Clark 2060 [W], Ecuador), (h) young fruits (from Bello 161 [INB], Costa Rica), (i) fruits (from Herrera et al. 1175 [MO, isotype], Panama); – scale = 1 cm, except g = 5 mm.

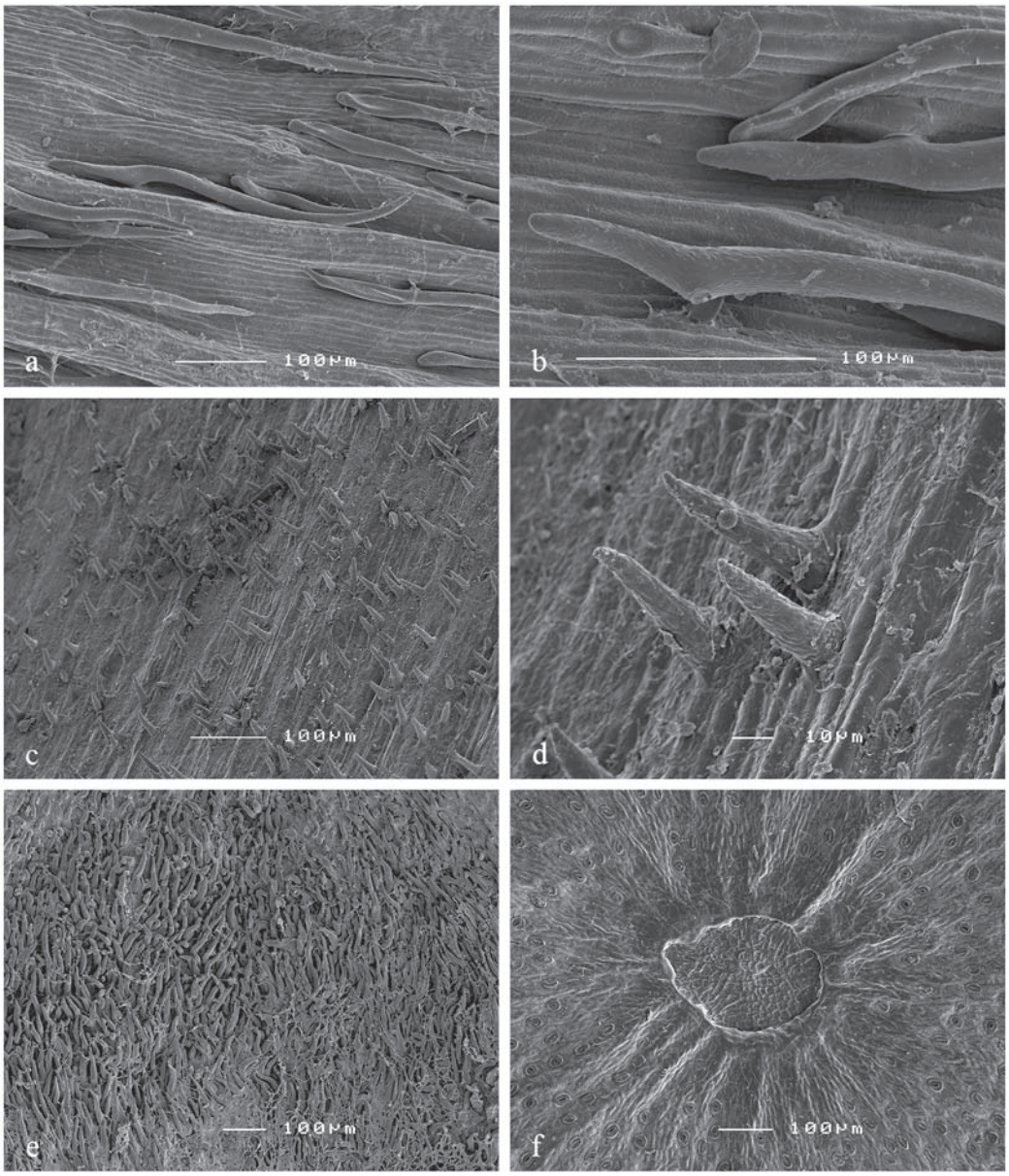

Fig. 3: *Diospyros juruensis*: (a–b) subsp. *hartmanniana*: two-armed hairs on abaxial side of a young leaf (from McPherson & Hensold 15310 [MO]); – (c–d) subsp. *campechiana*: minute hairs on a young twig (from Rovirosa 482 [NY]); – (e) subsp. *panamense*: layer of short hairs on the inside of a calyx (from Bello 161 [W]); – (f) subsp. *juruensis*: flachnectarium (extrafloral nectarium) on abaxial side of a leaf (from Marín 512 [W]); – (SEM-photographs: F. Brandstätter).

mm long, adnate to the corolla tube ca. 0.5 mm above its base; filaments 1–1.5 mm long and 0.4–0.6 mm wide, flat, glabrous on both sides, but densely hairy below the anthers and along the distal margins; anthers (1.5–) 3 mm long and ca. 0.8 mm wide, widest in the proximal third, tapering distally into a 0.8–1 mm long, subulate, warty, glabrous connective appendage; connectives especially abaxially densely covered on both sides (adaxial side of inner stamens rarely ± glabrous on some specimens) with long, ± spreading, ± straight (except some strongly curled hairs near base), blackish or light hairs; pollen sacks 2 mm long, often with appressed hairs laterally, opening by lateral slits (sometimes already in still closed flowers); rudiment of the ovary subglobose or flattened, 0.8–1.5 mm in diameter, usually 8-lobed or longitudinally ± grooved (impressions of filaments), without stylodia, glabrous proximally, with curled, short hairs on the sides and with a dense tuft of long, straight hairs distally or in subsp. *juruensis* completely glabrous, inside without structures; **female flowers** only available in subsp. *nenab* (Cárdenas 2109, fig. 2c; described in detail by Wallnöfer 1999): 7–8 mm long (pedicels excluded); bracts and bracteoles ca. 1.5 mm long and wide; calyx 4 mm long, 6 mm wide, undivided in the proximal 2 mm, lacking longitudinal ridges running down from the sinuses abaxially; sinuses between the lobes inconspicuous; calyx lobes 2 mm long, 3 mm wide, broadly rounded distally; corolla white when alive, brownish-black when dry, 7 mm long, glabrous on both sides; tube 5 mm long and 4 mm wide, widest shortly above the middle; corolla lobes ca. 2 mm long and 2.5 mm wide, broadly rounded distally; staminodia 8, ca. 5 mm long, adnate to the corolla tube 2 mm above its base, their free part narrowly lanceolate, tapering into a glabrous tip distally, densely hairy on the margins; ovary 2.6 mm in diameter, ± globose, glabrous, inside apparently anomalous in the only dissected flower; style (including stylodia) 2 mm long; stylodia two, ca. 1 mm long, with few appressed hairs in the area of their fusion; – old damaged (longitudinally fissured) female flowers of subsp. *panamense* (Bello 161): corolla ca. 5 mm long, glabrous, black when dry; aperture of the corolla ca. 2 mm wide; corolla lobes 2–3 mm long and 3 mm wide, rounded distally; staminodia not found; – female flowers of subsp. *campechiana* not available but described by Pacheco (1981) and Provance & Sanders (2009), extremely fragrant, corolla white, 8 staminodia reported; – female flowers of subsp. *hartmanniana* (Hammel et al. 17100): old flower buds (on twigs with young fruits) infected and anomalous inside; – applying to all subspecies: ovaries usually 4-locular (also in 5-merous flowers; fig. 5), rarely apparently 6-locular (as reported by Bello 732); style (including stylodia) on young fruits 1–2 mm long; stylodia two, ca. 0.5–1.5 mm long, distally longitudinally bent like an U, with the two edges prolonged in direction of the axis and on the outside often with a ± collar-like structure (fig. 4e, similar also to fig. 15E in Provance & Sanders 2009); stalk of the **fruits** up to 8 mm long and ca. 2 mm thick, still covered with indumentum; fruits (fig. 2, 5–7, 10–12) 1–3 (–7) per cyme, 1–4-seeded (fig. 5–6; – 4–6-seeded according to Bello 732), notably differing in size, ± globose when 4-seeded, disproportioned or asymmetrical when 2–3-seeded, ± ellipsoidal and strongly asymmetrical when 1-seeded, up to 2.5 cm (but usually much smaller) in diameter when dry, detaching with or without the calyx; mucro-like remnant of the style and stylodia 1–2 mm long; fruits green or cream when unripe, yellow, orange, reddish-orange or red when ripe, markedly smelling (Chávez 335, Pacheco 1981) and with a pleasant taste (Bello 732, Pacheco 1981), light brown, and smooth when dry; young fruits covered (at least at the apex) with an indumentum composed of hairs of different length or completely glabrous; fruit wall thin (ca. 0.2 mm thick when dry), becom-

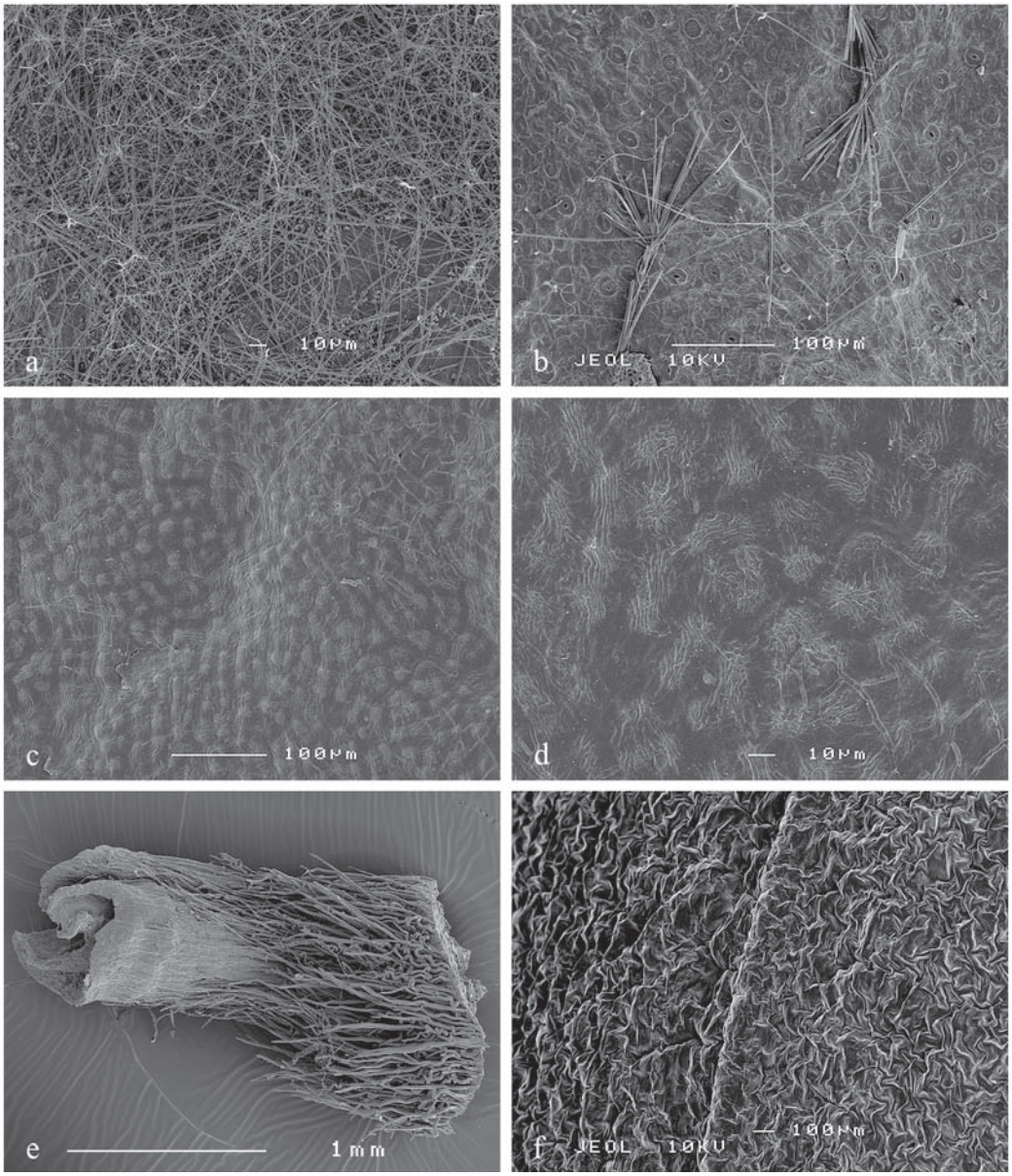

Fig. 4: *Diospyros juruensis*: (a) subsp. *campechiana*: crystal-needles interwoven with hyphae on adaxial side of a leaf (from Lundell 17840 [MICH]); – (b) subsp. *panamense*: crystal-bundles on abaxial side of a leaf (from Grayum et al. 5005 [FHO]); – (c–d) subsp. *juruensis*: subepidermal, minute granules on adaxial side of a leaf (from Marín 512 [W]); – (e–f) subsp. *panamense* (e) style and stylodia of a young fruit (from Bello 161 [W]), (f) surface of a seed around the longitudinal vascular strand (from Grayum et al. 5005 [FHO]); – (SEM-photographs: F. Brandstätter).

ing soft at maturity (mesocarp scanty), with the epidermis adhering when dry; seeds soon loose in the large, air-filled, smooth locules (causing a rattling noise when herbarium specimens are shaken; fig. 5); calyx green, coffee-brown (Bello 2442) or coffee-brown to yellowish (Fuentes 633) when alive, as a whole up to ca. 1 cm wide and up to ca. 0.5 cm high, ± dish- or bowl-shaped (sometimes on the outside markedly funnel-shaped near base), on the outside scattered to medium densely hairy, on the inside glabrous and ± wrinkled or covered (except near base) with a dense layer of short and thick, dark hairs, without longitudinal ridges on the outside; undivided (basal) part of the calyx ca. 2 mm long; lobes 3–5 mm long and 5–6 mm wide, usually thickened, ± flat on the margins, spreading or ± reflexed, broadly rounded distally; sinuses between the lobes inconspicuous, narrowly rounded (but some lobes often still imbricate); seeds ellipsoidal when single, ± like the segments of an orange or coffee-bean shaped when several in a fruit, 10 mm long, 5–7 mm wide, 4–6 mm thick, cream (Cárdenas 1164), green (Cárdenas 1026, Bello 634) or greenish-orange (Bello 732) when alive, brown when dry; outer tangential (periclinal) wall of the exotestal cells finely striate below the surface (these structures are therefore not visible on the SEM-photograph fig. 4f).

Notes: The populations ascribed here to *D. juruensis* sensu lato are displaying a large range of variation with respect to the size and shape of leaves, the indumentum and the appearance of the calyx and fruits. As there are all sorts of intermediates, no further separation of taxa at species level seems to be justifiable. Especially in Costa Rica and Panama speciation seems to be in full progress and hybridization may also occur frequently. – Some specimens are either in a bad condition, or the indumentum is heavily damaged, weathered, lost or encrusted with dirt and epiphytic cryptogams. In all these cases specimens have been tentatively assigned to one of the subspecies!

The black or blackish brown color of the indumentum in subsp. *campechiana* and *hartmanniana* seems to be due to the inclusion and accumulation (deposition) of naphthoquinones and their derivatives in the hairs. As can be seen from some specimens of the former subspecies (Contreras 5355, 6220), the indumentum is brown on the young bud apices, becoming dark brown more proximally and finally blackish brown or black on twigs, inflorescences and mature leaves.

The color of the dry leaves has been used for distinguishing taxa (González 2010, Provance & Sanders 2009) but it is an insecure feature, because it depends on the way the plant material has been preserved and on the duration of the drying-process. Due to the lack of drying equipment in the field, pressed, fresh plant material has often to be stored for a while in diluted alcohol for preservation. In such cases, color-changes of the dry specimens are striking.

As flowering specimens are not well represented in herbaria, a comprehensive study of morphological features is to date not possible. Specimens with female flowers are even rarer and were available only in subsp. *nenab*. The length and shape of the style and stylodia and the degree of their fusion have been used by Provance & Sanders (2009) in their determination key. But as female flowers are rarely available and stylodia on fruits are mostly broken or heavily damaged (often longitudinally split), it was not possible to study them in detail. Not all of the drawings shown in Provance & Sanders (2009: fig. 15) seem to be true to nature. Whether or not the style and stylodia can be used for the delimitation of taxa has yet to be proven. Female flowers are urgently needed for study! Specimens pertaining either to subsp. *juruensis* or to subsp. *panamense* with male flowers only, cannot be distinguished to date.

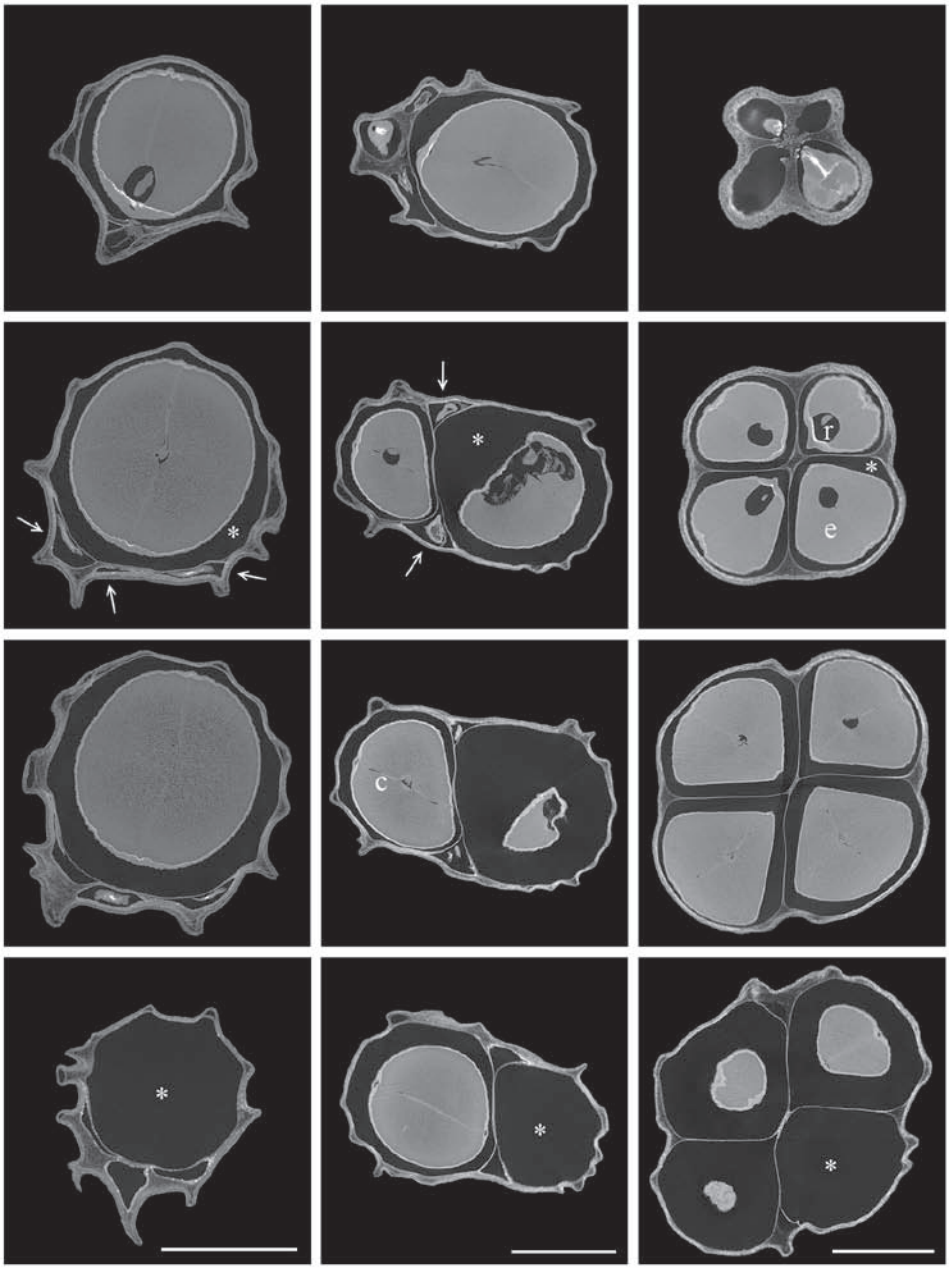

Fig. 5: *Diospyros juruensis* subsp. *panamense*: cross-sections (via X-ray tomography) of an one-seeded (left column), a two-seeded (centre) and a four-seeded (right column) fruit (all from Haber & Bello 6738 [W]) taken with a MicroXCT-200 from the company XRadia Inc.; – 1st row: from distal part, 2nd and 3rd row: from areas around and below middle and 4th row: from proximal part of fruits; arrows pointing towards the small locules containing one, aborted seed each; c: cotyledons; e: endosperm; r: cavity containing the radicula; *: air-filled space; bar = 5 mm; – (photographs: Y. M. Staedler, processed by B. Wallnöfer).

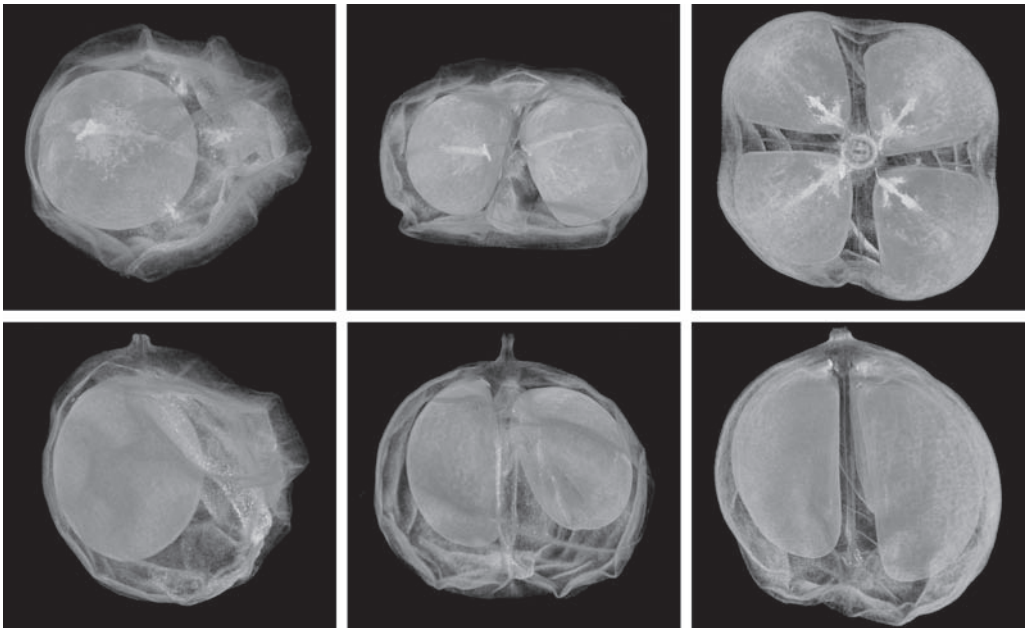

Fig. 6: *Diospyros juruensis* subsp. *panamense*: three-dimensional reconstruction (via X-ray tomography) of a one-seeded (left column), a two-seeded (centre) and a four-seeded (right column) fruit (all from Haber & Bello 6738 [W], same fruits as shown in fig. 5); – 1st row: as seen from above, 2nd row: as seen from the side (styles pointing upwards); – (reconstructions: Y. M. Staedler).

The fruits are usually two-carpellate, four-locular and 4-seeded if perfect (fig. 5–6). Frequently 1–3 seeds per fruit do not develop and the corresponding locules stop growing. The latter are subsequently pushed towards the sides of the enlarging fruits (fig. 5). This seems to be a rare feature among other species of *Diospyros*, where locules with aborted seeds always extend up to the central axis of the fruits. Therefore, fruits of *D. juruensis* s.lat. often become disproportioned or strongly asymmetrical and are of notably differing size (fig. 5–6; see also fig. 6 in Provance & Sanders 2009). Despite the fact that the shape of fruits is varying very much and is thus an insecure feature, Provance & Sanders (2009) used it as the main differentiating character in their determination key.

The fruits seem always to turn orange or red when mature (see also Ibarra-Manríquez & Cornejo-Tenorio 2010). The thin fruit wall becomes somewhat soft at maturity (mesocarp scanty). The seeds are soon becoming loose in the large, air-filled, smooth locules (fig. 5–6) and are causing a rattling noise upon shaking of herbarium specimens. This seems also to be a rare feature among species of *Diospyros*. It is not clear what biological function this could have. As many herbarium vouchers have been collected on wet or frequently inundated places or along rivers, a possible explanation could be that water may also play an important part in dispersing the floating fruits but this has still to be proven (this possibility has also been considered by Provance & Sanders 2009). Birds have also been seen to eat the fruits (Haber 2000, Haber & Bello 6738). Two collectors (Chávez 335 and Bello 732) as well as Pacheco (1981) mentioned that the fruits were

very fragrant ("muy olorosos") and their taste sweet and pleasant. This could suggest that other animals (nocturnal mammals?) may eat them too. As can be seen from many herbarium specimens, at least some fruits detach from the calyx (compare also Provance & Sanders 2009). It is however not yet clear whether this always applies to all populations when fruits are mature.

Note: the species is highly variable and the following subspecies are not well supported and seem quite vague. Further studies may prove that they cannot be maintained.

Key to subspecies

1 Inflorescence and infructescence axes covered with brown or dark brown hairs 2
1* Inflorescence and infructescence axes covered with blackish-brown or black hairs 4

2 Leaves narrowly lanceolate, 4–5 times longer than wide; NW-Colombia (and possibly also SE-Panama) ..... subsp. *nenab*
2* Leaves lanceolate to elliptic, sometimes oblong, less than 3.6 times longer than wide 3

3 Fruits (except calyx) completely glabrous; Brazil, Peru and Costa Rica .. subsp. *juruensis*
3* Fruits at least around the apex medium densely to densely hairy; Costa Rica, Panama and Ecuador (Esmeraldas) ..... subsp. *panamense*

4 Petioles (9–) 10–18 mm long; leaf-lamina (5–) 10–27 cm long and (2.5–) 5–8 (–9.8) cm wide; male inflorescences markedly branched, expanded, multi-flowered (but not known from Oaxaca); southern Mexico and Guatemala ..... subsp. *campechiana*
4* Petioles 4–8 (–10) mm long; leaf-lamina (1.2–) 3–12 cm long and (0.8–) 2–6 cm wide; male inflorescences contracted, 1–6-flowered; Costa Rica and Panama .... subsp. *hartmanniana*

Diospyros juruensis* subsp. *juruensis; [fig. 1, 2a, 3f, 4c–d, 8–9].

Typus: see above.

= *Diospyros crotalaria* Provance & A.C.Sanders, J. Bot. Res. Inst. Texas 3 (1): 95–98, fig. 6, 15A (2009).
Typus: Costa Rica, Puntarenas, Cantón de Osa, R.F. Golfo Dulce, Península de Osa, Rancho Quemado, sector oeste, 400 m, 8°41'10" N, 83°35'10" W, creciendo en la fila [mountain ridge], (fr), 9 Sep. 1992, **J. Marín 512** [holotype: MO n.s. (Provance & Sanders 2009: fig. 6, 15A), isotypes: CR n.s., INB n.s., K n.s., W 2×], "árbol 20 m × 15 cm DAP; corteza gruesa; frutos amarillos".

Tree up to 18 m tall and with dbh up to 15 cm; petioles 5–7 (–10) mm long; leaf-lamina (2–) 7–20 (–25.5) cm long and (1.2–) 3–7 cm wide, lanceolate to broadly lanceolate or elliptic; inflorescence axes covered with a brown indumentum; male inflorescences divaricately branched and up to ca. 50-flowered on the Brazilian type, more contracted on Peruvian specimens (not known from Costa Rica); female inflorescences up to 6-flowered; young fruits (except calyx) glabrous, slightly shiny. – Very unfortunately, Provance & Sanders (2009) did not make public how they distinguish their Costa Rican "*D. crotalaria*" from *D. juruensis*.

Figures: twigs, leaves, flowers, fruits (Provance & Sanders 2009: fig. 1B, 1D, 6, 10–11, 15A).

Distribution, habitat, and phenology: It is known from Puntarenas in Costa Rica, from Loreto in Perú, and from the type collection only in Amazonas (Brazil), (fig. 8–9). A distribution map for Costa Rica is given in PROVANCE & SANDERS (2009: fig. 14). In Costa Rica it was collected at elevations of 200–782 meters, in Perú and Brazil at 95 to ca. 150 meters. – The growth places (riparian forests, bosques ribereños) in Loreto are described as; "located at natural levee maximally flooded a few months annually (restinga), but traversed by several meters deep ravines (bajiales) often flooded more than a half year annually (tahuampa); flooded by a mixture of white water from the Ucayali river and black water from local upland streams" (Ruiz et al. 8248, 6371, etc.). In the Brazilian state of Amazonas it was collected on várzea land, and in Costa Rica on mountain ridges ("fila"). – In Amazonas (Brazil) and in Loreto (Peru) it has been found flowering in June and October, respectively. In Costa Rica it has been collected in fruit in August, September, and from November to January. In Loreto (Peru) it is reported with young fruits from November.

Vernacular names: In Loreto (Peru) it is called "polvora caspi" (Anonymous RI.lat 6-2-77 [= Freitas 24]).

Specimens examined: **Costa Rica**, Puntarenas, Cantón de Osa, R.F. Golfo Dulce, Península de Osa, Cerro Chocuaco, camino al faro, 400 m, 8°43'20" N, 83°32'20" W, (fr), 28 Dec. 1993, **R. Aguilar 2877** [CR n.s., INB n.s., K n.s., MO n.s., W], "árbol 10 m × 13 cm DAP; frutos maduros rojos"; – Golfito, Parque Nacional Esquinas, sección "Bosque de los Austriacos" [near the Biological Station La Gamba], Fila way, 200 m, 8°41' N, 83°13' W, (fr), 15 Jan. 1998, **W. Huber & A. Weissenhofer 843** [CR n.s., LI 2×, W, WU], "tree 10 m; fruits bright orange"; – same locality and collectors: (st), 27 Mar. 1999, **1574** [W], "tree 4 m"; (yfr), 1 Aug. 1999, **1678** [CR n.s., W, WU 3×], "tree 12–13 m; fruits greenish"; – Cantón de Golfito Jiménez, Dos Brazos de Río Tigre, siguiendo el sendero entre las quebraditas, Cerro Müeller (falso Müeller) hasta Cerro Rincón, 782 m, 8°30'35" N, 83°28'15" W, (fr), 25 Nov. 1990, **G. Herrera 4647** [CR n.s., K, MEXU, MO], "árbol de 18 m × 15 cm DAP; follaje cartáceo de envés opaco; cáliz verde; fruto amarillo".

Perú, Loreto, Prov. Loreto, Distrito Nauta, Reserva Nacional Pacaya - Samiria, Río Yanayacu, Cocha Cocamilla, 95 m, 4°48'59" S, 74°10'28" W, restinga, (yfr), 12 Nov. 1992, **C. Del Carpio, O. Tovar & J. Ruiz 1719** [MO], "árbol 18 m; frutos inmaduros, verdes"; – along the lower Ucayali river, ca. 7 km W of the Jenaro Herrera village, "Zona de Braga", 120 m, 4°55' S, 73°45' W, located at natural levee maximally flooded a few months annually (restinga), but traversed by several meters deep ravines (bajiales) often flooded more than a half year annually; flooded by a mixture of white water from the Ucayali river and black water from local upland streams, (yfr), 1 Sep. 1993 – 12 Feb. 1994, **J. Ruiz M., L.P. Kvist & L. Freitas A. 8716** [MO], "tree 6 m tall; 85 mm dbh"; – same locality, data and collectors: (st), **1125** [MO], "tree 16 m tall; 139 mm dbh"; – (st), **1263** [MO], "tree 5 m tall; 153 mm dbh"; – (flbuds male), **2397** [MO], "tree 8 m tall, 95 mm dbh"; – (defl male), **4163** [MO], "tree 16 m tall, 96 dbh"; – (st), **8248** [MO], "tree 5 m tall; 99 mm dbh"; – (yfr), **9344** [MO], "tree 9 m tall; 90 mm dbh"; – same area and collectors: "Zona de Lobillo", 120 m, 4°59' S, 73°44' W, plot flooded up to several meters and often for more than a half year annually (tahuampa); mostly flooded by black water from local upland streams, but occasionally also by white water from the Ucayali river, (defl male), 1 Sep. 1993 – 12 Feb. 1994, **6371** [MO], "tree 8 m tall, 107 mm dbh"; – Prov. Requena, Jenaro Herrera, 125 m, 04°55' S, 73°40' W, bosque ribereño alto, (fl male), 11 Oct. 1988, **Anonymous RI.lat 6-2-77 (= Freitas 24)** [FHO, G n.s., W], "árbol 10 m, DAP 12 cm; flores verde-amarillentos".

***Diospyros juruensis* subsp. *campechiana* (LUNDELL) B.WALLN., comb.n.**; – [fig. 7, 3c–d, 4a, 8].

≡ *Diospyros campechiana* LUNDELL, Contr. Univ. Michigan Herb. 4: 23 (1940).
Typus: Mexico, Campeche, Palizada, [ca. 18°22' N, 91°52' W; according to CAMPOS-RÍOS & CHIANG CABRERA (2006): 18°15'0" N, 92°4'60" W], in swamp side [in swamp

Fig. 7: Holotype of *Diospyros juruensis* subsp. *campechiana* (LUNDELL) B.WALLN. [MICH].

forest], (fr), 25–28 Jul. 1939, **E. Matuda 3843** [holotype: MICH (photo NY: N.S. 6901 at FHO, NY), isotypes: A, F (photo F 52491), K, LL, MEXU n.s., MICH, MO n.s., NY, US], "arbor alt. 7–10 m, diam. 40–45 cm".

= *Diospyros camposii* PROVANCE & A.C.SANDERS, J. Bot. Res. Inst. Texas 3 (1): 93–95, fig. 4, 15C (2009).
Typus: Mexico, Oaxaca, Dto. Miahuatlán, Mpio. San Jerónimo Coatlán, 41,5 [correct seems to be ca. 13] km al SW de San Jerónimo Coatlán [Miahuatlán?], brecha a Progreso, 1550 m, 16°10‘ N, 96°59‘ W, bosque de pino-encino alterado; suelo amarillo arcilloso, (fr), 29 Nov. 1990, **A. Campos V. 3452** [holotype: CHAPA n.s. (PROVANCE & SANDERS 2009: fig. 4), isotype: MEXU], "árbol 25 m, abundante; fruto anaranjado".

Tree up to 20 m tall and with dbh up to 35 cm; bark of twigs with or without patent, whitish-translucent, stiff, minute hairs (fig. 3c–d); petioles (9–) 10–18 mm long; leaf-lamina (5–) 10–27 cm long and (2.5–) 5–8 (–9.8) cm wide, lanceolate to broadly lanceolate or ± elliptic, often oblong; inflorescence axes usually covered with a brownish-black or black indumentum; male inflorescences divaricately branched and up to ca. 50-flowered; female inflorescences 1–3 (–7)-flowered (7-flowered on Contreras 5355 at DS); young fruits (except calyx) completely glabrous (except on the populations from Oaxaca, see below); compare also the descriptions in PACHECO (1981), WHITEFOORD & KNAPP (2009) and PROVANCE & SANDERS (2009).

In Veracruz (Mexico) it has a disjunct distribution and is known only from pastures and secondary forests ("acahuales") in a small geographic area, where only few, isolated individuals can be found (PACHECO 1981). As the fruits are edible (as stated by the aforementioned author), it may have been introduced there by man in the pre-Columbian era. The hairs on the infructescences of these populations are brown to dark brown but not typically black. This can, however, also be seen in some other collections.

Isolated populations occurring at elevations of 1200–1550 meters in a small area in Oaxaca (Mexico) are documented by fruiting specimens only. PROVANCE & SANDERS (2009) assigned them to their new taxon "*D. camposii*". The petioles are quite long ranging from 10 to 15 mm and the infructescence axes are covered with blackish hairs. The fruits are often 1-seeded and asymmetrical, 1.8–2.5 cm long and 1.5–2.5 cm in diameter. Their apices bear brown hairs around the base of the old styles and are sometimes ± glabrescent. The calyx lobes are 4 mm long, 5 mm wide, and flexed downwards towards the axis, a feature which can sometimes also be seen on specimens from other populations. These plants from Oaxaca are assigned here provisionally to subsp. *campechiana*, although they could also be placed within subsp. *hartmanniana*. To clarify the situation, flowers of both sexes are urgently needed for study!

Figures: twigs, leaves, flowers, fruits (PROVANCE & SANDERS 2009: fig. 1A, 2, 3, 4, 15B–C,); twig with fruits (LUNDELL 1942: fig. 5, from the holotype but strongly modified); leaf and fruit (PACHECO 1981: fig. 1c–d); pollen (AYALA-NIETO & LUDLOW-WIECHERS 1983: plate 1–2).

Distribution, habitat, ecology, and phenology: This subspecies is known from southern Mexico (Veracruz, Tabasco, Campeche, Chiapas, Oaxaca), and from Guatemala (Petén, Alta Verapaz, Izabal), (fig. 8), where it was collected from sea level up to an elevation of

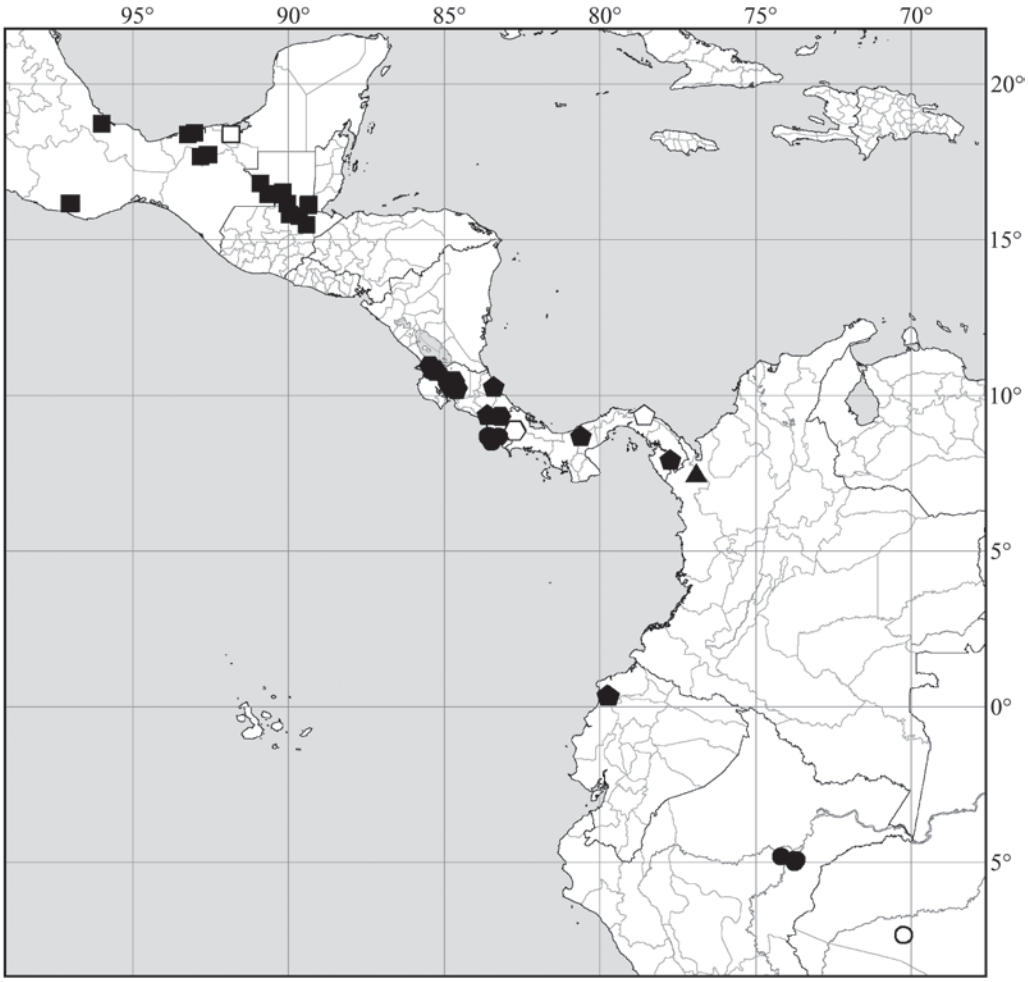

Fig. 8: Distribution of *Diospyros juruensis* subsp. *juruensis* (●, type locality: ○); subsp. *campechiana* (■, type locality: □); subsp. *hartmanniana* (⬢, type locality: ⬡); subsp. *nenab* (▲); subsp. *panamense* (⬟, type locality: ⬠).

160 meters. Isolated populations occurring in a small area in Oaxaca are growing at elevations of 1200–1550 meters. A distribution map is given in Provance & Sanders (2009: fig. 5), and another for Veracruz in Pacheco (1981) and in Angulo & Soto (1990). – It grows in semideciduous (see also Zamora Crescencio et al. 2008) or evergreen, high or low forests, in floodplain forests, along rivers, in swamp forests, or on wet land. It has been found in primary forests called zapotales (climax forest dominated by *Manilkara zapota*; sensu Lundell 1937) but also in secondary forests ("acahuales") and some more deteriorated vegetation ("semi-chaparral") and on pastures (potreros). The climatic requirements are specified in Angulo & Soto (1990). In Oaxaca it is reported to grow in mesophyllous forests, in woods with *Pinus* and *Quercus* and in gullies (cañadas), on yellowish, clayey or black soil. – It has been found flowering in April, May, August and

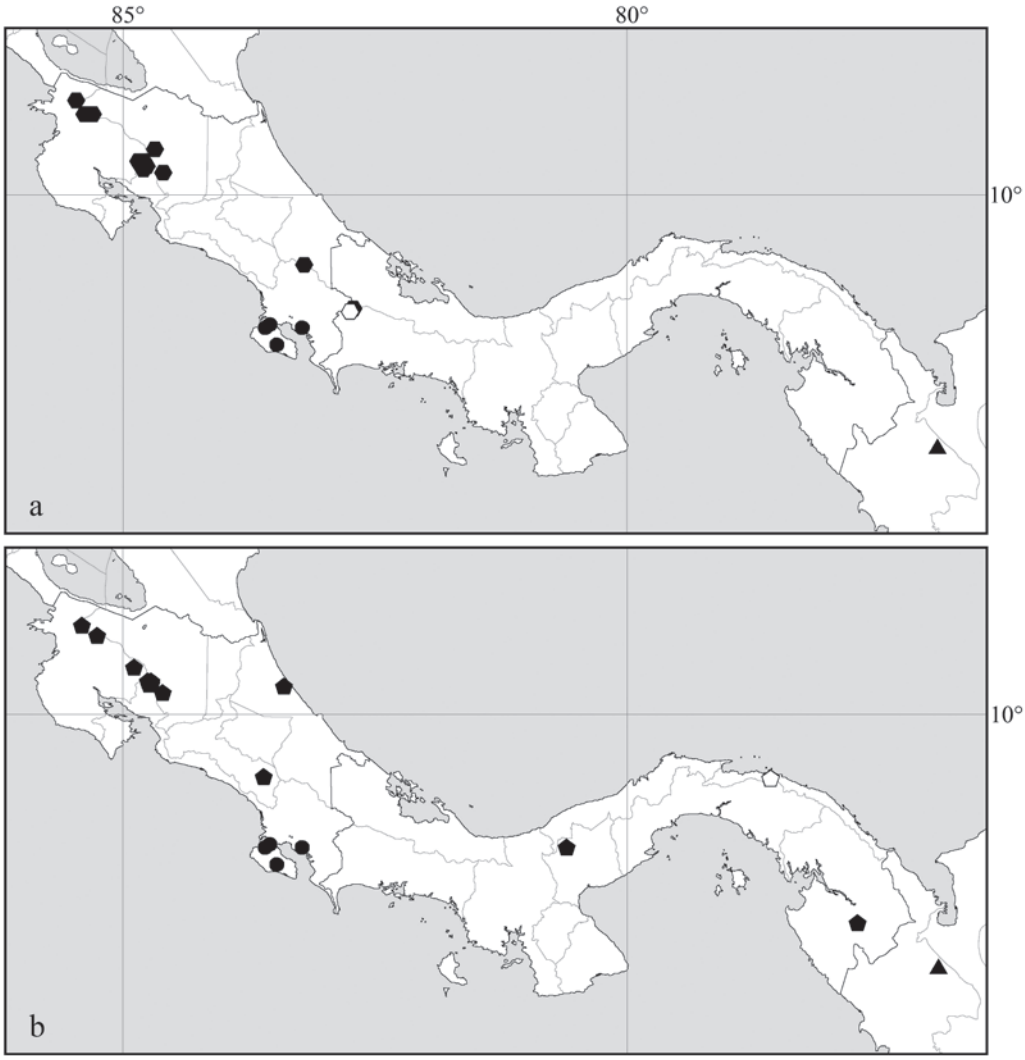

Fig. 9: Distribution of *Diospyros juruensis* subsp. *hartmanniana* (a) and of subsp. *panamense* (b) in Costa Rica and Panama (for symbols see fig. 8).

September, and fruiting in February, and from July to November. In Oaxaca (Mexico) it has been collected in fruit from November up to January.

Vernacular names and use: In Tabasco it is called "cafeillo de playa" or "cafecillo de playa" (PACHECO 1981, ANGULO & SOTO 1990), "chilillo" (Gilly et al. 343), or "palo prieto" (Rovirosa 482), and in Veracruz it is known as "zapotillo" (Martínez-Calderón 1555), or "zapotito" (PACHECO 1981). The fruits are edible but now only scarcely used (PACHECO 1981).

Specimens examined: **Mexico**, Veracruz, Mun. Ignacio de la Llave, 50 m, [18°43' N, 95°59' W], acahual; suelo arcilloso, (fr), 13 Nov. 1967, **G. Martínez-Calderón 1555** [A, CAS, CHAPA n.s., F, FHO 2×, MEXU n.s., MICH, MO, USF n.s., XAL n.s.], "árbol; fruto amarillo". – Tabasco, Mun. Comalcalco, San Cayetano,

0 m, [18°22' N, 93°13' W], potrero, (fr), 27 Nov. 1983, **F. Ventura A. 20796** [CAS, MO, XAL n.s.], "árbol 15 m, escaso; fruto rojo"; – ad margines fluvii Gonzalez, [18°25' N, 93°1' W], (fl male), 8 May 1889, **J.N. Rovirosa 482** [K, NY, PH, US]; – Municipio de Jalapa, 4 km de la desviación carretera Jalapa-Tacotalpa, 10 m, [17°40' N, 92°49' W], potrero, (fr), 22 Nov. 1983, **F. Ventura A. 20785** [BM, CICY, MO, NY, XAL n.s.], "árbol 15 m, escaso; fruto rojo"; – Mun. Macuspana, along Arroyo Hular, S of Macuspana, [ca. 17°43' N, 92°36' W], (fr), 28 Sep. 1944, **C.L. Gilly, S. Hernandez X. & E. Hernandez X. 343** [MICH], "3 m tall, 5 cm diam.; fruit turning from yellow to red when collected"; – 8 km de la entrada de Macuspana hacia Escárcega y 1,5 km al norte, [added in CICY: 17°43'00" N, 92°33'30" W], selva inundable, orillas del río, asociado con *Pachira*, *Bactris*, (fr), 25 Aug. 1981, **M.A. Magaña A. & S. Zamudio 358** [CICY n.s. (photocopy), XAL n.s.], "árbol 8–10 m, escaso; frutos amarillos y naranjas". – Chiapas, Mun. Ocosingo, a 3 km S de Frontera Corozal [= Frontera Echeverria] paralelo al Río Usumacinta, 120 m, [16°48' N, 90°53' W], selva alta subperennifolia, (fr), 17 Aug. 1984, **E. Martínez S. 7326** [CAS, CHAPA n.s., GH, MEXU n.s., W], "árbol 20 m; fruto amarillo"; – Mun. Ococingo [= Ocosingo], en la zona Marqués de Comillas, a 6 km SE de Ejido Benemerito de las Americas, con rumbo a Flor de Cacao, 160 m, [16°27' N, 90°38' W], selva alta subcaducifolia, (fr), 10 Oct. 1984, **E. Martínez S. 8159** [MEXU n.s., W], "árbol 18 m; fruto amarillo". – Oaxaca, Dto. Miahuatlán, Mpio. San Jerónimo Coatlán, 12,3 km al N de Piedra Larga, sobre el camino a Progreso, la desviación se encuentra 9,6 km al NE de Piedra Larga, carr. a Miahuatlán, 1200 m, 16°9'00" N, 97°1'00" W, bosque mesófilo en bosque de pino, en cañada, (fr), 16 Dec. 1987, **R. Torres C. & A. Campos 10895** [F, MEXU, MO, RSA], "árbol 15 m, poco frecuente; fruto amarillo"; – Mpio. Piedra Larga, 12,5 km al NE de Piedra Larga, sobre el camino a El Progreso, 1300 m, 16°10' N, 97°1' W, bosque mesófilo; suelo negro, (fr), 15 Dec. 1987, **A. Campos V. & R. Torres C. 825** [F, MEXU, MO, RSA, UEC], "árbol de 20 m, abundante; fr. verde y amarillo"; – Mpio. San Jerónimo Coatlán, 41 [correct seems to be ca. 13] km al SW San Jerónimo Coatlán [Miahuatlán?], 1250 m, 16°10' N, 96°58' W, cañada de bosque mesófilo; suelo amarillo arcilloso, (fr), 17 Jan. 1988, **A. Campos V. 1017** [F, MEXU, MO, RSA], "árbol 8 m, abundante; fruto anaranjado".

Guatemala, Petén, Rio Pasion, Altar de Sacrificios, [16°28' N, 90°32' W], in high forest on bank of river, (fr), 8 Feb. 1964, **C.L. Lundell 17840** [F n.s., FHO (fragm.), GH n.s., IJ n.s., LL, MICH, MO, P, S, US n.s.], "tree 60 ft. high, 14 in. in diam.; fruits ellipsoid, orange"; – across river from Sayaxché, 50 m, [16°31' N, 90°10' W], semi-chaparral area, (flbuds male), 5 May 1942, **J.A. Steyermark 46306** [A n.s., US], "tree 30 ft. tall; leaves subcoriaceous, deep green above, dull paler green beneath"; – Brecha Chinajá, 12 km from Laguna Petexbatun, [ca. 16°26' N, 90°10' W], high forest, (fl male), 20 May 1965, **E. Contreras 5401** [LL, MO], "tree ca. 50 ft., 12 in. diam.; flowers white"; – along Río Machaquila, N of El Cambio, 75–100 m, [ca. 16°9' N, 90°1' W], (flbuds male), 25 Apr. 1942, **J.A. Steyermark 45974** [A n.s., MO, NY, US], "tree 30 ft.; leaves firmly membranous, dark green above, paler green beneath; flowers greenish"; – La Cumbre, on Pusila road, 5 km N, [16°8' N, 89°20' W], acahual, (yfr), 19 Aug. 1976, **C.L. Lundell & E. Contreras 20224** [CAS, LL, MO, UCR n.s.], "tree 30 ft., 6 in. diam.; fruit green, yellow-orange latex"; – La Cumbre, km 142 of Cadenas Road, [16°5' N, 89°21' W], low forest on wet land, (fr), 24 Sep. 1966, **E. Contreras 6220** [BRIT, DS, F n.s., LL], "tree 35 ft., 4 in. diam.; fruits orange-yellow"; – La Cumbre, Caserio Sapurul, bordering Arroyo Sapurul, [16°5' N, 89°21' W], in zapotal, high forest, (fl male), 7 Apr. 1977, **C.L. Lundell & E. Contreras 20739** [LL, MO, WIS n.s.], "tree 60 ft., 15 in. diam.; latex orange; flowers white". – Alta Verapaz, Sebol, bordering Rio Sebol, [15°48' N, 89°57' W], in high forest of corral, (fl male), 27 Apr. 1964, **E. Contreras 4519** [DS, G, LL, US], "small tree 20 ft. high, 3 in. diam.; flowers white"; – same area, coordinates and collector: in high forest, (fl male), Aug. 1964, **5354** [DS, F n.s., G, LL, MO], "small tree; flowers white"; – in high forest along river, (fr), Aug. 1964, **5355** [DAV, DS, F n.s. (dig. photo), G, IJ n.s., LL, MO, US], "tree"; – Chahal, bordering Rio Chiyú, 1 km west, [15°45' N, 89°39' W], in low forest, (fr), 29 Oct. 1968, **E. Contreras 8032** [F n.s., G 2×, LL, MO, US], "tree 40 ft. high, in 12 in. diam.; fruits orange". – Izabal, Ensenada de Los Lagartos, extremo N de lago Izabal, Creekes, 1 m, [15°28' N, 89°24' W], selva media perennifolia inundable, (fl male), 1 Sep. 1988, **E.M. Martínez, W.D. Stevens, A.N. Díaz & H. Droege 23380** [MO], "árbol 6 m; flor blanca".

***Diospyros juruensis* subsp. *hartmanniana* (S.Knapp) B.Walln., comb.n.**; – [fig. 10, 2b, 3a–b, 8–9].

≡ *Diospyros hartmanniana* S.Knapp, Novon 7 (3): 256–258, fig. 1 (1997).

Typus: Panama, Chiriquí, near Costa Rican border, ca. 13 road-km from Río Sereno, Finca Hartmann, 1550–1750 m, 8°50' N, 82°45' W, forested slopes [protologue: cloud

forest], (fr), 23 Oct. 1992, **G. McPherson & P.M. Richardson 15959** [holotype: BM, isotypes: FHO, MO, PMA n.s. (dig. photo)], "tree 12 m; fruit green to yellow-orange".

= *Diospyros haberi* Provance & A.C.Sanders, J. Bot. Res. Inst. Texas 3 (1): 98–101, fig. 7, 15D (2009).
Typus: Costa Rica, Alajuela, Cantón de Upala, P. N. Rincón de la Vieja, Cordillera de Guanacaste, sendero La Siembra, ca. a 7 km de la casa de Administración, 1500 m, 10°47'50" N, 85°18'19" W, (fr), 6 Jul. 1991, **G. Rivera 1422** [holotype: MO n.s. (Provance & Sanders 2009: fig. 7B, 7D), isotype: K n.s.], "árbol de 12 m × 30 cm DAP; frutos verdes inmaduros".

Tree up to 28 m tall and with dbh up to 60 cm; petioles 4–8 (–10) mm long; leaf-lamina (1.2–) 3–12 cm long and (0.8–) 2–6 cm wide, lanceolate to broadly lanceolate or elliptic; inflorescence axes covered with brownish-black or black, usually persisting hairs; male inflorescences contracted, 1–6-flowered; female inflorescences 1 (–2)-flowered; young fruits (except calyx) covered only near base and apex with less than 0.5 mm long, black hairs, but on some small-leaved collections (see next paragraph) completely glabrous; compare also the description in Whitefoord & Knapp (2009).

Trees growing on open and exposed places, such as "windswept forest on cliff edge" (Haber & Daniel 9895), "cliff edge and canyon slopes" (Hammel et al. 17100), "en pequeño tapaviento" [small windbreak belt] (Bello 1124), and in pastures (potreros) (Dryer 1240, Haber & Bello 5023, 5028, 7323, Haber et al. 5015), are developing due to the difficult environmental conditions particularly small leaves [(1.5–) 3–8 cm × (0.8–) 2–3.5 cm]. Specimens from such plants have been called "*D. haberi*" by Provance & Sanders (2009). The type of the latter (see their fig. 7B, 7D) matches well the one of subsp. *hartmanniana* (fig. 10). The study of specimens of that subspecies reveals a gradual transition from small leaved individuals to such with larger leaves. Other morphological characteristics (e.g., indumentum on calyces) are also quite variable. As can be seen from the distribution map of "*D. haberi*" presented by the above mentioned authors (fig. 14), there seems to be no substantial difference in distribution with respect to subsp. *hartmanniana*.

Figures: flower buds, stamens, twig with fruits (Knapp 1997: fig. 1); twigs, leaves, flowers, fruits (Provance & Sanders 2009: fig. 1C, 7, 8A–B, 15D). As Zamora Villalobos et al. (2004) omitted to cite the collections on which their drawings are based, the latter cannot be assigned to any subspecies.

Distribution, habitat, ecology, and phenology: This subspecies is known from Costa Rica (Guanacaste, Alajuela, and Puntarenas), and from Panama (Chiriquí), (fig. 8–9). A distribution map is given in Provance & Sanders (2009: fig. 14), but the taxonomic circumscription used by these authors is different from the one adopted here. Subspecies *hartmanniana* was collected at elevations of 1000–1800 (ca. 2200) meters and was recorded to grow in premontane or lower montane, tropical, moist forests, in cloud forests, on forested slopes, cliff edges, canyon slopes and along rivers. Several specimens were collected in pastures. – The flowers are pollinated by moths ("non-hawkmoth") and the fruits dispersed by birds (Haber 2000). – It has been found flowering from May to July, and fruiting from January to April, and from July to November (with young fruits in May and June).

Fig. 10: Holotype of *Diospyros juruensis* subsp. *hartmanniana* (S.Knapp) B.Walln. [BM], (insert: the writing on the folder).

Vernacular names: In Costa Rica it is called "fruta de pavo" (González 2010) but this may apply to subsp. *panamense* (compare there).

Specimens examined: **Costa Rica**, Guanacaste, Parque Nacional Guanacaste, Estación Cacao, Liberia, 1100 m, 10°55'45" N, 85°28'15" W, (fr), 2 Nov. 1990, **C. Chávez 335** [CR n.s., INB n.s., MO], "árbol 15 m × 30 cm DAP; frutos inmaduros verdes, otros dorados, maduros amarillos muy olorosos"; – P. N. Rincon de la Vieja, slope on the pacific side, on the way to the top, 1300 m, 10°48' N, 85°23' W, (fr), 13 Feb. 1998, **W. Huber H104** [LI 2×, W], "tree 20 m; fruits orange"; – Cantón de Tilarán, Cañitas, Río Cañas, lado Pacífico, 1200 m, 10°20' N, 84°51' W, en pequeño tapaviento, (yfr), 25 Aug. 1989, **E. Bello 1124** [FHO, INB, MO], "árbol 28 m × 60 cm DAP; fuste negro con manchas blancas; frutos verdes crema"; – Guanacaste, Monteverde, 1550 m, 10°48' N, 84°59' W, [correct seems to be: ca. 10°20' N, 84°48' W], cloud forest, (st), 13 Jul. 1990, **A.H. Gentry, W. Haber, L. Woodruff & B. Boyle 71605** [paratypes: BM n.s., MO], "tree"; – same data and collectors: **71605a** [MO]. – Alajuela, San Carlos, La Fortuna, Finca El Jilguero, cumbre de Volcán Chato, bajando por el sector de las Chorreras, 1140 m, 10°26'35" N, 84°41'25" W, (fr), 27 Nov. 1992, **G. Herrera 5669** [K n.s., MO], "árbol 10 m × 15 cm DAP; frutos inmaduros amarillos, maduros rojo-anaranjado"; – Reserva Biológica Alberto Ml. Brenes, 1100 m, 10°13' N, 84°36' W, premontane tropical forest, (st), 11 Aug. 2000, **J. Homeier 465** [BIEL n.s., INB n.s., USJ n.s., W], "tree". – Puntarenas, Monteverde, San Luis river valley below community, Pacific slope, 1000 m, 10°20' N, 84°50' W, in pasture; premontane moist forest, (flbuds male), 9 May 1986, **W.A. Haber, E. Bello C. & L. Lierheimer 5015** [MO, W], "tree 20 m; flowers white"; – same area: 1400 m, 10°20' N, 84°50' W, in pasture; lower montane wet forest, (fl male), 9 Jun. 1986, **W.A. Haber & E. Bello C. 5023** [MO, W], "tree; flowers white"; – same data and collectors: (fl male), **5028** [MO, W], "tree; flowers white"; – Cordillera de Tilarán, Monteverde, Comunidad, 1400–1500 m, [10°18' N, 84°49' W], en potrero abierto, (fr), 18 Mar. 1977, **V.J. Dryer 1240** [MO], "árbol 7 m; frutos amarillo-anaranjados con 1 semilla grande (mas rojo-anaranjados al madurar)"; – Cantón de Puntarenas, Monteverde, cliff edge above Quebrada Máquina, along Fonseca, Hotel de Montaña and Savage farms, 1100–1300 m, 10°18' N, 84°48' W, moist forest; windswept forest on cliff edge, (fl male), 3 Jun. 1990, **W. Haber & S. Daniel 9895** [FHO, INB, MO], "tree 8 m; calyx green; corolla white; flowers male"; – Monteverde, Bajo Tigre Reserve, Pacific slope, 1200–1300 m, 10°18' N, 84°48' W, moist forest; forest understory, (fr), 3 Apr. 1991, **W. Haber & W. Zuchowski 10600** [CR n.s., FHO 2×, INB, MO], "tree 12 m; fruit orange, with soft rind when mature; calyx dark green with black hairs"; – Monte Verde to San Luis Valley, along Río San Luis, 1000–1400 m, 10°17' N, 84°07' W, [correct seems to be: 10°17' N, 84°49' W], cliff edge and canyon slopes along rio, (flbuds female, yfr), 14 Jul. 1988, **B. Hammel, W. Haber & W. Zukowski 17100** [CR n.s., F n.s., FHO, INB n.s., MO, W], "tree 25 m, 30 cm dbh; slash with foul odor of urine; flowers sordid white; fruits becoming bright orange"; – Cord. de Tilarán, San Luis, Buen Amigo, 1100 m, 10°16'33" N, 84°47'45" W, (fr), 4 Mar. 1994, **Z. Fuentes 633** [INB, MO, W], "árbol 6 m; frutos anaranjados; cáliz café-amarillo"; – Monteverde Reserve, Nuboso Trail, 1550 m, [10°17' N, 84°48' W], forest understory, (flbuds male), 27 May 1981, **W. Haber 546** [CR n.s., MO], "med. tree; mature fruits orange"; – Ojo de Agua - Monteverde, Finca Leonel Hernández, 1600 m, 10°17' N, 84°46' W, potrero, (fl male), 19 Jun. 1987, **W. Haber & E. Bello 7323** [FHO 2×, MO, W], "árbol 10 m × 35 cm DAP; flores blancas"; – valley of Río San Luis, just S of Monte Verde, 1000–1200 m, 10°16' N, 84°48' W, in woods along the river, (yfr), 18 Jun. 1985, **B. Hammel & W. Haber 13937** [MO n.s., W], "tree 25 m, 50 cm dbh; leaves glossy, slightly paler below; fruits green"; – Quebrada Veracruz, Finca Pablo Morales, vertiente Pacífica, 1600 m, 10°15' N, 84°48' W, dentro del bosque, (fr), 11 Jan. 1990, **E. Bello 1767** [FHO, MO], "árbol 12 m × 20 cm DAP; frutos crema"; – Monteverde, Vert. Pacífico, 1520–1580 m, [10°15' N, 84°48' W], en vegetac. secundaria al lado del camino por la Reserva, (fr), 9 Feb. 1977, **V.J. Dryer 1178** [MO], "árbol 7 m; frutos amarillentos con 1 semilla grande"; – Monteverde, in pacific slope forest below community, 1100 m, [10°15' N, 84°48' W], slope forest, (fl male), 23 May 1981, **W. Haber 542** [CR n.s., MO], "med. tree; fruits orange"; – Cantón de Buenos Aires, Olán, siguiendo filas en cuenca superior de Río Cabagra, 1700 m, 9°17'40" N, 83°11'50" W, (fr), 24 Sep. 1989, **G. Herrera 3542** [FHO, INB, MO], "árbol 8–10 m × 20 cm DAP; follaje verde intenso; frutos inmaduros verde".

Panama, Chiriquí, Cerro Pando area, ca. 2200 m, 8°52' N, 82°43' W, (fr), 24 Aug. 1982, **C. Hamilton et al. 969** [paratypes: BM n.s., FHO, MO], "tree 20 m; fruit green"; – near border with Costa Rica, ca. 13 road-km from Río Sereno, Finca Hartmann, 1400–1800 m, 8°50' N, 82°45' W, forested slopes, (yfr), 12 May 1991, **G. McPherson & N. Hensold 15303** [paratypes: BM, FHO 2×, MO, PMA n.s. (dig. photo)], "tree 6 m; fruit green, old fruit brown"; – same data and collectors: (fl male), **15310** [paratypes: B n.s., BM, CAS n.s., FHO, MO, PMA n.s. (dig. photo)], "tree 7 m; corolla white".

***Diospyros juruensis* subsp. *nenab* (B.Walln.) B.Walln., comb.n.**; – [fig. 11, 2c–d, 8–9].

≡ *Diospyros nenab* B.Walln., Ann. Naturhist. Mus. Wien, B, 101: 579–581 (1999).
Typus: Colombia, Chocó, Mun. de Riosucio, zona de Urabá, Cerros del Cuchillo, sector Cuchillo Negro, orilla quebrada Cedros, 10 m, [7°30‘ N, 76°55‘ W], potreros y bosque perturbado, (fr), 9 Feb. 1988, **D. Cárdenas 1164** [holotype: MO, isotype: JAUM n.s.], "arbusto 3 m; fruto amarillo; semilla crema; cáliz verde".

Treelet 3–4 m tall; petioles 5–9 mm long; leaf-lamina (2.8–) 9.5–15.3 cm long and (1.1–) 2–3.5 cm wide, narrowly lanceolate, 3.5–4.8 times longer than wide; inflorescence axes covered with brown hairs; male flowers unknown; female inflorescences 1–3 (–4)-flowered; for female flowers see above in the general description; young fruits (except calyx) glabrous. – A full description and a list of specimens are given in Wallnöfer (1999). Additional specimens and observations are urgently needed to ascertain whether or not the leaves are always narrow and the plants low. At least the reduced size could be due to human activities in the forests.

Distribution, habitat, and phenology: It is only known from a small area in northwestern Colombia (Chocó), where it was collected at elevations of 10–200 meters (fig. 8–9). It has been found in primary or disturbed forests, along mountain streams (quebradas) and on pastures (potreros). – It has been collected with flowers in June, with young fruits in January and November, and with older fruits in February.

***Diospyros juruensis* subsp. *panamense* (S.Knapp) B.Walln., comb.n.**; – [fig. 12, 2e–i, 3e, 4b, e–f, 5–6, 8–9].

≡ *Diospyros whitei* S.Knapp, Novon 7 (3): 258–260, fig. 3 (1997), **non** *Diospyros whitei* Dows.-Lem. & Pannell, Bull. Jard. Bot. Belg. 65 (3–4): 399–403 (1996).

≡ *Diospyros panamense* S.Knapp, Novon 9 (4): 524 (1999).
Typus: Panama, San Blas, Río Diablo y vecindad de Duque Sui, a unos 10 km de la costa frente a la Isla de Nargana, ruta hacia Cerro Ibedón, 80–110 m, 9°22‘ N, 78°35‘ W, (yfr), 1 Jul. 1992, **H.B. Herrera, R. Obladia & N. Blanco 1175** [holotype: BM, isotypes: FHO 2×, MO, PMA n.s.], "árbol 5 m; frutos verdes".

Tree up to 26 m tall and with dbh up to 50 cm; petioles 4–8 mm long; leaf-lamina (3.7–) 7–18 (–24) cm long and (1.5–) 2.5–8.2 cm wide, lanceolate to broadly lanceolate or ± elliptic; base of lamina usually cuneate, but on some collections from the area near the Atlantic coast rounded (Bristan 1229) or narrowly truncate (Shrank & Molina 4284 and Folsom 3168); inflorescence axes covered with brown or dark brown, soon weathering hairs; male inflorescences contracted and up to 6-flowered (Costa Rica and Panama, fig. 2h–i, 12) or expanded and multi-flowered (Ecuador, fig. 2f); female inflorescences 1–2 (–6)-flowered; very young fruits covered on the whole surface with up to 1–1.5 mm long, brown (in vivo said to be golden) hairs (fig. 2h–i); older fruits covered with a persistent indumentum at the apex and on the styles, glabrescent in the middle and at the base (except on areas protected from abrasion); compare also the description in Whitefoord & Knapp (2009). – The subscalariform (ladder-like) venation pattern referred to by Knapp (1997) can only be seen on older leaves and seems not always distinctive. In addition it can also be found on some leaves of subspecies *hartmanniana*.

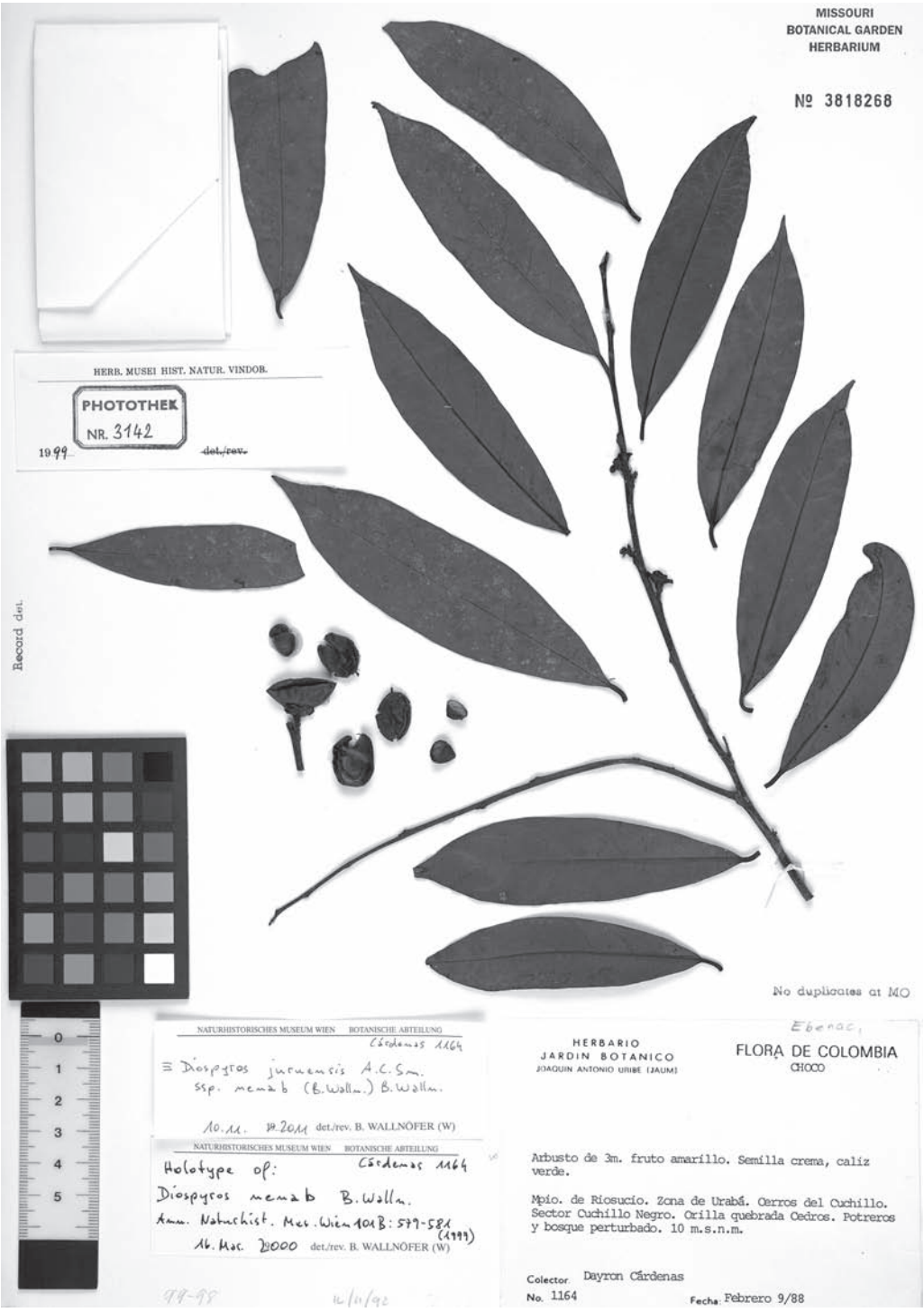

Fig. 11: Holotype of *Diospyros juruensis* subsp. *nenab* (B.WALLN.) B.WALLN. [MO].

On several specimens (e.g. Bello 634, Haber et al. 6087) the indumentum (its density as well as the color and length of hairs) appears to be intermediate between subspecies *panamense* and *hartmanniana*. It is not clear whether or not this is due to frequently occurring hybridization. Some other specimens are either in a bad condition or the indumentum is heavily damaged. In all these cases specimens have been tentatively assigned to one of the subspecies.

The collections Aguilar et al. 2727 and Aguilar 2749 are very atypical (Provance & Sanders 2009: fig. 12; Zamora Villalobos et al. 2004; – the sterile specimen Aguilar 4644 seems also to belong here), and display the following characters: leaves very large, 25 cm long and 10 cm wide; inflorescence axes and calyces of male flowers covered with light to dark brown hairs; fruits exceptionally large, reaching 3 cm in diameter, glabrous (as the surface of the three fruits available is not any more immaculate, it is not clear whether there ever was an indumentum); calyx lobes ± flexed downwards towards the axis (the spreading, hair-like structures on them seem to be fungi); fruit wall apparently much thicker; seeds free, producing a rattling noise when the fruits are shaken. Both collections have been gathered near a house ("junto a la casa") and most likely belong to plants cultivated for fruits by indigenous people! Additional information and more collections are necessary to evaluate these plants. The placement under subspecies *panamense* is therefore just provisional.

Figures: twig, leaves, fruit (White 1978: fig. 5); twig with young fruits (Knapp 1997: fig. 3); twig, leaves, flowers, fruits (Provance & Sanders 2009: fig. 8C, 9, 12, 13, 15E–F). According to the data supplied on distribution and phenology, the drawings in Zamora Villalobos et al. (2004) seem to be based on the atypical collections Aguilar et al. 2727 and Aguilar 2749.

Distribution, habitat, ecology, and phenology: This subspecies is known from Costa Rica (Guanacaste, Alajuela, Limón, San José and Puntarenas), from Panama (Coclé, San Blas, and Darién), and from one small area in Ecuador (Esmeraldas) (fig. 8–9). A distribution map for Costa Rica and Panama is given in Provance & Sanders (2009: fig. 14), but the taxonomic circumscription used by these authors is different from the one adopted here. The subspecies *panamense* was collected in Costa Rica and Panama at elevations of 550–1210 meters (with exception of the type: 80–110 m, and Shank & Molina 4284: 0 m), and in Ecuador at 400–600 meters. – In Costa Rica and Panama it grows in premontane wet forests (bosque pluvial premontano), in wet cloud forests, in swampy areas ("bosques pantanosos-yolillosos" [Yolillo-palm = *Raphia taedigera*]), along rivers, and rarely also in pastures (potreros). In Esmeraldas (Ecuador) it is reported to be a canopy tree in premontane wet, primary forests on slopes and along streams in ravines. – The flowers are probably pollinated by moths ("non-hawkmoth") (Haber 2000). According to Haber & Bello 6738 ("había 4 pavoncillos comiendo los frutos") and Haber (2000), the fruits are eaten and dispersed by birds. – In Costa Rica it has been found flowering in May and December, and in Ecuador from January to April. In Costa Rica and Panama it has been collected fruiting in May, and from July to February, and in Ecuador from August to November.

Vernacular names: In Alajuela (Costa Rica) it is called "fruto de pavo" (Bello 732); (but see also under subsp. *hartmanniana*).

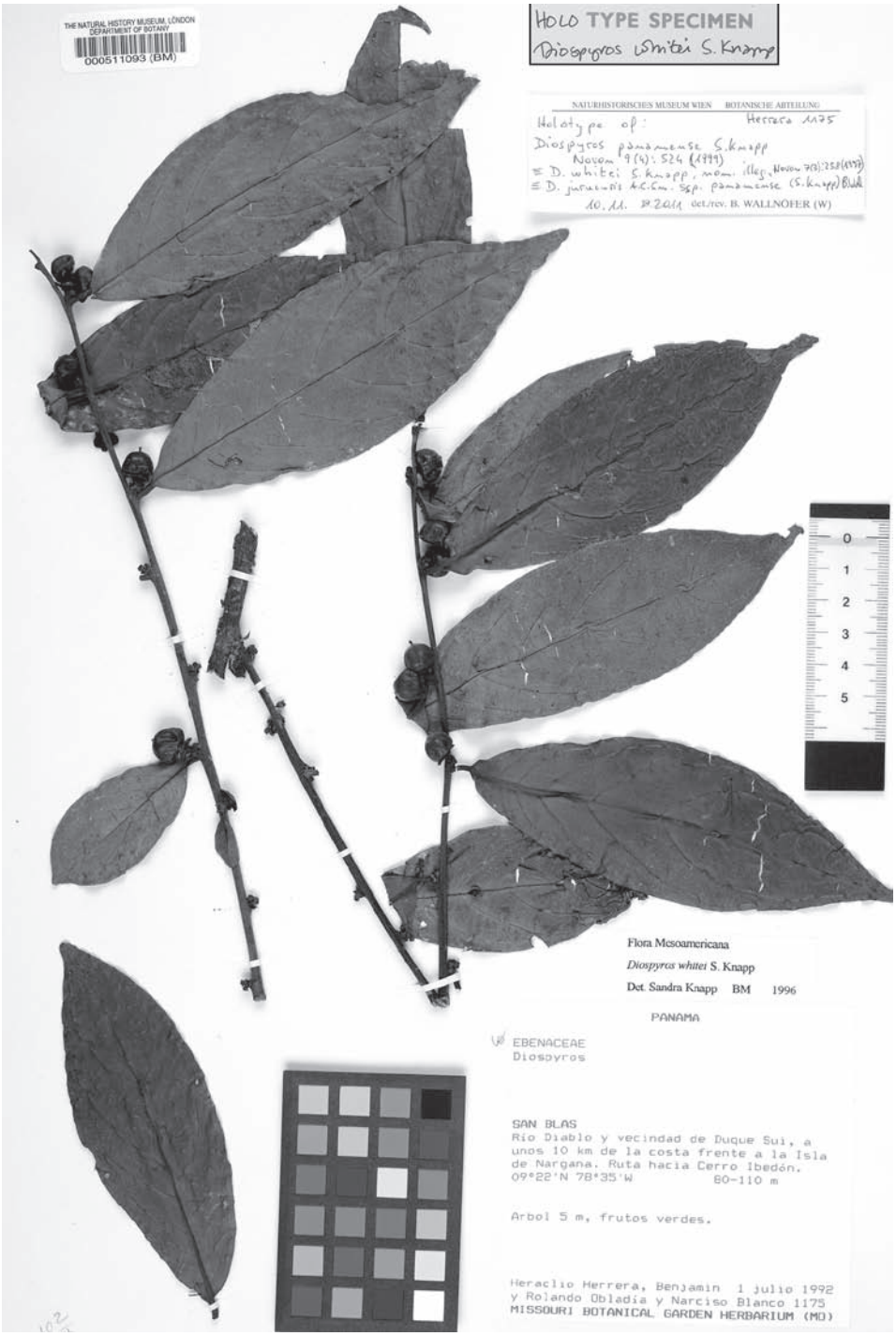

Fig. 12: Holotype of *Diospyros juruensis* subsp. *panamense* (S.KNAPP) B.WALLN. [BM], (insert: the writing on the folder).

Specimens examined: **Costa Rica**, Guanacaste, large patch of remnant primary forest on W slope of Cerro Nubes, ca. 2 km E of Silencio de Tilarán, ca. 900 m, 10°28' N, 84°53' W, primary forest, in disturbed spot, (fr), 26 Jan. 1985, **M. Grayum, G. Herrera & P. Sleeper 5005** [FHO, MO], "branch found on ground; very tall trees looming overhead; fruits bright yellow-orange, rather hard, containing 4 large coffee-bean shaped seeds". – Alajuela, Cantón de Upala, P. N. Guanacaste, Cordillera de Guanacaste, estación San Ramón, Dos Ríos, sector La Campana, 550 m, 10°52'50" N, 85°24'05", (flbuds male), 1 May 1993, **R. Espinoza, R. Zúñiga & D. García 884** [INB n.s., K n.s., MO n.s., W], "árbol 9 m × 25 cm DAP; flores blanco-cremoso"; – P. N. Rincón de la Vieja, sendero a la Quebrada Mora, camino a la Colonia Blanca, 840 m, 10°46'32" N, 85°15'10" W, (fr), 30 Nov. 1990, **G. Rivera 920** [INB n.s., K n.s., MO n.s., W], "árbol 20 m × 19 cm DAP; fuste liso; corteza negra; frutos anaranjados"; – Reserva Biológica Monteverde, Río Peñas Blancas, 900 m, 10°20' N, 84°43' W, bosque pluvial premontano, (fr), 3 Feb. 1987, **W.A. Haber & E. Bello C. 6738** [FHO, INB, MO, W], "árbol 20 m × 40 cm DAP; frutos amarillos, de 13 mm de diámetro; había 4 pavoncillos comiendo los frutos"; – same area, data and collectors: 850 m, (fl male), 22 May 1987, **7148** [CR n.s., FHO 2×, MO, W], "rama caída del árbol; flor blanca, anteras café"; – same area and collectors: Atlantic slope, farm of Wilson Badilla S., 800–900 m, 10°20' N, 84°45' W, rain forest; this tree in pasture, (fr), 1 Dec. 1986, **6498** [FHO, MO], "tree 25 m; fallen fruit cream, 20 mm"; – same area: atlantic slope, 800–900 m, 10°20' N, 84°43' W, rain forest edge, (fr), 3 Oct. 1986, **W. Haber, H.P. Bello & E. Cruz 6087** [CR n.s., FHO, MO], "tree 20 m; fruit green, 1 cm diam."; – same area: 900 m, 10°19' N, 84°44' W, (fl male), 12 May 1987, **W. Haber & E. Cruz 7107** [CR n.s., FHO, INB, MO, W], "árbol 20 m; flores blancas"; – same area and collectors: Finca Wilson Salazar, 800 m, 10°18' N, 84°43' W, potrero, (fr), 7 Nov. 1987, **7696** [CR n.s., FHO 2×, INB, MO, W], "árbol 20 m; frutos verdes"; – same area and collectors: Fila de Toro, sendero Pipilacha y Campo Tres, 900–1100 m, 10° N, 84° W, [10°18' N, 84°43' W], (fr), 21 Jan. 1991, **10632** [CR n.s., FHO, INB, MO], "árbol 20 m; frutos naranja"; – same area: Finca de Eladio Cruz, 820 m, 10°19' N, 84°43' W, orilla del bosque, (fr), 24 Feb. 1989, **E. Bello 732** [FHO, MO], "árbol 20 m × 28 cm DAP; fuste negro; fruto 22 mm diam., 23 mm de largo, inmaduro color crema, maduro naranja de sabor agradable, carnosidad blanca que se oxida naranja al contacto con el aire; 4–6 semillas verde naranja"; – same locality and collector: (fr), 2 Oct. 1990, **2442** [CR n.s., FHO, INB, MO], "árbol 12 m × 30 cm DAP; cáliz café; frutos crema"; – same area and collector: Parcela de Rockwell, 820 m, 10°19' N, 84°43' W, orilla del bosque, (fr), 21 Dec. 1988, **634** [CR n.s., FHO 2×, INB n.s., MO, W], "árbol 26 m × 45 cm DAP; fruto crema de 24 mm de diam., con dos o tres semillas verdes; savia crema"; – same area and collector: vertiente Atlántica, 900 m, 10°18' N, 84°44' W, rama caída dentro del bosque, (yfr), 13 Jul. 1988, **161** [CR n.s., FHO, INB, MO, W], "árbol, flor seca; frutos iniciales"; – same area and collector: parcela de los enanos, 850 m, 10°18' N, 84°44' W, (yfr), 2 Sep. 1988, **351** [MO 2×], "árbol caido dentro del bosque; fruto café"; – Reserva de San Ramón, Río San Lorencito, 800 m, [ca. 10°13' N, 84°36' W], (fr), 2–6 Oct. 1986, **J.A. Chacón & Q.M. Chacón 2328** [MO], "árbol 20 m, 50 cm DAP; frutos verde amarillo". – Limón, Suerre y Dos Bocas, Drenajes de los Ríos Parismina y Reventazón, 0 m, [10°17' N, 83°24' W], bosque lluvioso, pantanoso-yolilloso [Yolillo-palm = *Raphia taedigera*], (fr), 3 Oct. 1951, **P.J. Shank & A. Molina R. 4284** [GH], "árbol 6 m". – San José, Cantón de Perez Zeledon, Cordillera de Talamanca, Las Nubes, Santa Elena, 1210 m, 9°23'30" N, 83°35'50" W, creciendo a orilla del río, (fr), 3 Aug. 1995, **E. Alfaro 291** [INB n.s., MO n.s., W], "árbol 10 m × 8 cm DAP; frutos verde-amarillos". – Puntarenas, Cantón de Osa, R. F. Golfo Dulce, Cuenca Térraba-Sierpe, Bahia Chal., La Parcela, 150 m, 8°43'50" N, 83°27'17" W, (st), 3 Aug. 1996, **R. Aguilar 4644** [INB], "árbol 8 m × 7 cm DAP, estéril; corteza negra"; – Fila Costeña, Río Piedras Blancas, junto a la casa, faldas Cerro Anguciana, Fila Cruces, 900 m, 8°49'02" N, 83°11'23" W, (fr), 9 Dec. 1993, **R. Aguilar, D. Gómez, M. Grayum & B. Hammel 2727** [INB n.s., MO n.s., K n.s., W], "árbol 20 m × 40 cm DAP; corteza negra; frutos verde brillante"; – same place: (flbuds male), 10 Dec. 1993, **R. Aguilar 2749** [CR n.s., INB n.s., K n.s., MO n.s., W], "árbol 15 m × 25 cm DAP; corteza negra; botones florales blancos".

Panama, Coclé, New Works at Rivera sawmill, Alto Calvario, 600–800 m, [8°41' N, 80°36' W], wet cloud forest trees of medium to large size, (yfr), 12 May 1977, **J.P. Folsom 3168** [paratype: MO], "tree of 1–1.5 feet dbh; fruit turning yellow"; – Darién, Cerro Pirre, [7°56' N, 77°43' W], (yfr), 4 Aug. 1967, **N. Bristan 1229** [paratypes: FHO, MO 2×, NY, US], "árbol; madera suave; fruto verde".

Ecuador, Esmeraldas, Quinindé Cantón, Estación Biológica Bilsa (Bilsa Biological Station), Montañas de Mache, 20 km NW of Quinindé and 3 km W of Santa Isabela, downstream (SW) in ravine below (ESE) cabin, 600 m, 00°22' N, 79°45' W, premontane wet forest (bosque húmedo, premontano); along stream in ravine, (fr), 18 Sep. 1994, **J.R. Abbott 15188** [MO, QCNE n.s. (dig. photo)], "branches on ground, tree not found; fruits purple-black"; – same area and Station: 35 km W of Quinindé, 5 km W of Santa Isabel, SE ridge trail, 400–600 m, 00°21' N, 79°44' W, premontane wet forest; canopy tree in mature forest, (fr), 15 Sep.

1994, **J.L. Clark & B. Adnepos 96** [COL n.s. (dig. photo), K, MO, QCNE n.s. (dig. photo), W], "canopy tree; mature fruits orange"; – same area and coordinates: Invader trail, 400–600 m, (fr), 18 Nov. 1994, **J.L. Clark, H. Lintz & S. Mora 278** [COL n.s. (dig. photo), K, MO, QCNE n.s. (dig. photo), W], "tree 9 m; mature fruits orange"; – same area and coordinates: 400–600 m, (fl male), 24 Jan. 1995, **J.L. Clark 419** [COL n.s. (dig. photo), K, MO, QCNE n.s. (dig. photo), W], "tree 10 m"; – same data and collector: 500 m, (fr), 2 Oct. 1996, **J.L. Clark 3011** [COL n.s. (dig. photo), K, MO, QCNE n.s. (dig. photo), US n.s., W], "tree 15 m; calyx truncate; fruits greenish orange"; – same area and coordinates: 400–600 m, (yfr), 26 Mar. – 11 Apr. 1995, **J.L. Clark & Y. Troya 508** [K, MO, QCNE n.s. (dig. photo), W], "tree 15 m"; – same area and coordinates: 500 m, (fl male), 6 Feb. 1996, **J.L. Clark, N. Kerber & J. Plihal 2060** [COL n.s. (dig. photo), K, MO, QCNE n.s. (dig. photo), W], "tree 17 m, 12.4 inches dbh; flowers white and extremely fragrant"; – same area and coordinates: 500 m, (st), 30 Mar. 1996, **J.L. Clark, K. Berg & J. Leffingwell 2377** [MO, W], "tree 15 m, DBH 8.6 inches"; – same data: (st), **2379** [MO, W], "tree 10 m, DBH 6.3 inches", and: (st), **2383** [MO, W], "tree 8 m, DBH 3.9 inches"; – same area and coordinates: 500 m, 00°21' N, 79°44' W, (st), 20 Mar. 1998, **J.L. Clark & C. Pallis 4852** [MO n.s., GUAY n.s. (dig. photo)], "tree 16 m tall; bark slash forms black ring"; – same area and coordinates: 500 m, (fr), 8 Aug. 1997, **H. Vargas, D. Neill & T. Núñez 1469** [MO n.s., QCNE n.s. (dig. photo)], "árbol de 13 m, 42 cm de DAP; frutos verdes"; – same data and collectors: (fr), **1472** [MO, QCNE n.s. (dig. photo), W], "árbol 8 m, 46 cm DAP; frutos axilares verdes"; – same area and coordinates: Cube River (NE corner of station), 500 m, (fl male), 11 Mar. 1998, **J.L. Clark, C. Pallis & J. West 4631** [MO n.s., QCNE n.s. (dig. photo)], "subcanopy tree; bark slash forms black ring; flowers extremely fragrant; corolla white and tubular (slightly urecolate)"; – same area and coordinates: forest W of cabin, 400–600 m, (fr), 26 Sep. 1994, **N. Pitman 726** [K, MO, QCNE n.s. (dig. photo), W], "tree 8 m, 15 cm dbh, growing on a slope; bark black, inner bark orange, wood white, rank-smelling; fruits green, orbicular, 2 cm diam."; – same area: 550 m, 00°21'13" N, 79°42'00" W, (fr), 24 Nov. 1999, **D. Neill & QCNE botany interns 12230** [MO n.s., QCNE n.s. (dig. photo)], "tree 15 m tall, 14 cm diameter; black inner bark; fruits green, fleshy"; – same area: 580 m, 00°21'36.7" N, 79°42'40.4" W, bosque primario nublado, húmedo premontano, (fl male), 18 Feb. – 5 Mar. 1995, **W. Palacios, J. Clark & N. Jaramillo 13508** [K, MO, QCNE n.s. (dig. photo), W], "árbol 15 m, 20 cm DAP; copa ancha y densa; hojas disticas; corola crema".

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